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The Natural Control of Insect Populations[1]

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Introduction

Animals are capable of multiplying their numbers by some form of reproduction; but they are hindered by natural means from multiplying to the point of committing collective suicide by exhausting the resources of this planet. Animals are also subject to having their numbers decreased; but, likewise, their decrease to extinction is hindered by natural means. The question of these natural means of limiting increase and decrease of numbers is a fundamental problem of Ecology: the problem of the mechanism of natural control of populations. The solution of this problem has, of course, great practical interest because man suffers from some animals being too few (beneficial species) and others too numerous (pests).

It is necessary to be clear as to what is meant by the term "control". To the economic entomologist the term usually means limitation of insect numbers to density levels which are not significantly injurious to man's material interests. It is true that most insect populations are naturally so limited, at least in respect to increase. But this definition logically requires that all populations outside such levels must be out of control, i.e., bound to increase to the point of collective suicide or decrease to zero, which is palpably untrue. Many insect populations injure man's interests yet neither increase nor decrease unrestrainedly. A more satisfactory definition of control emerges not from the viewpoint of man's material interests but from the viewpoint of the continuing existence of the population itself.

For present purposes, a population may be defined as the number of individuals of a particular species existing in a particular area. Populations do disappear naturally from some areas, temporarily or permanently in the human time scale. But these are relatively rare occurrences. Provided the areas studied are not too small or emigration/immigration precluded, field populations generally remain continuously in being. No population, of course, persists at a constant density of individuals. Density fluctuates between variable higher and lower values. Obviously, if a population is to remain in being, the highest densities must always be below the level resulting in collective suicide, and the lowest densities must always be above zero. Control simply means the arresting of increase and decrease short of these extinction levels. The levels at which arrest occurs may or may not be in man's interest. The economic entomologist's "control" is therefore control occurring at economic levels. It will be noted that my definition of control is factual and not confounded with theory as to how it comes about (cp. Nicholson, 1933, who apparently defines control as the production of balance between population and environment).

Modern study of population dynamics may be said to have begun with the famous essay of Malthus (1798). Since then, many workers have provided field data, more or less useful but always incomplete, on the factors determining numbers for individual species. Others have studied artificially simplified popu-

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lation systems in the laboratory. Some have advanced differing general theories of natural control which have been attacked and defended robustly. The quest goes on, and the student today is confronted with an ever-growing literature which is a disheartening morass of insufficient facts, alleged facts, ill-defined terminology and conflicting theories.

Perhaps the most useful reviews of work on natural control are those of W. R. Thompson (1939) and M. E. Solomon (1949). The subject can not be covered comprehensively in a short paper. I propose to examine, very briefly, the theories of Thompson (1929), Nicholson (1933) and Andrewartha & Birch (1954). The reasons for this choice should be fairly obvious. The prevailing theory seems to be Nicholson's, which is somewhat similar to Smith's (1935). Among theories differing from Nicholson's, those of Thompson and of Andrewartha & Birch are the most comprehensive. I shall deal with the three theories in chronological order, and end with my own theory.

The Theory of Thompson

Thompson's theory (1929), reaffirmed in his discussion (1939, 1956) of other population theories, suffers when condensed. This is to be expected since he holds that "the causes of natural control . . ., [being] essentially multiple and variable, [are] difficult to bring within the compass of any simple definition". I doubt if even the following longish extracts from his writings will convey his view adequately:

"Populations are not self-governing systems. Natural control . . . is primarily due . . . to the intrinsic limitations of the organisms themselves. Every organism has . . . specific needs. An environment which meets these specific needs is, for a given species, the optimum environment. Given the optimum environment, indefinite increase at a specific rate is possible. [But] at a given moment, in a given area, the precise environmental complex constituting the optimum for a given species will be found at relatively few points. This is the real reason why organisms . . . do not often increase to the point [i.e., level of numbers] where they are devastating plagues."

"When conditions in a locality inhabited by a given species approach the optimum, the species automatically increases in numbers . . . but it obviously can not go on increasing indefinitely. As it increases in numbers it necessarily spreads, both in space and time. As it spreads, it moves to points outside its optimum environment, when its rate of multiplication immediately diminishes. Furthermore, as the population of the species becomes more numerous, the action it exerts upon its environment, both indirectly and directly, increases in intensity, producing changes which are on the whole, in so far as they depend purely and simply on the numerical increase, disadvantageous, since they consist to a great extent in the progressive exhaustion of the nutritive power of the environment in relation to the species considered. It must also be remembered that the condition of the globe at any point is never constant. A region which today presents conditions optimum for a given species may depart from optimum conditions in the direction X next year and in the direction Y in the year following. Thus, under even most favourable conditions, there can not be a continuous and uninterrupted increase in numbers but simply an oscillating movement."

"Outbreaks of species are simply due to the fact that conditions momentarily correspond or approximate to the ecological optimum; control means simply a departure in one or many directions from the optimum. [These conditions of course include biotic factors but] the discontinuity and variability in habitats produced by the physical factors is undoubtedly the primary extrinsic factor of natural control. [However] as a general rule, the complex of factors [conditions] which actually effects control in the case of any species differs in composition from point to point and from year to year in the area of distribution. It follows that there is not in general any [particular] regulating factor [or factors] responsible for the natural control of a species. . . . The

causes of natural control even for a particular species [being] essentially multiple and variable [are] difficult to bring within the compass of any simple definition."

"The fundamental constitution of the universe, composed of a multitude of specifically different and interacting things, living and non-living, necessarily implies a limited possibility of existence for any particular one of them. The fact that there are species, that is, a variety of essentially limited things, means that their ability to increase is necessarily limited. . . . When we recognize the specific intrinsic limitations of organisms we have, in my opinion, arrived at the absolutely fundamental explanation of natural control: that is to say, of the fact that no organism increases without limit. This is a philosophical explanation which, indeed, verges on the metaphysical, and this I think is a sign that we have really got to the bottom of the subject."

A minor criticism of Thompson's theory may be made on his peculiar use of the word "optimum". The term suggests an environment in which organisms can fulfil themselves completely, i.e., live healthily, realize their reproductive capacities to the full, and die of old age. Clearly he does not mean this since he is well aware that a population will increase when comparatively few or no individuals enjoy truly optimum conditions. By "optimum" conditions he obviously means conditions favourable to population increase.

A major criticism is that Thompson pays too little attention to the concept of density dependent factors. Apart from the reference (see above) to disadvantageous progressive exhaustion of the nutritive power of the environment by increasing numbers, he dismisses this not altogether unimportant facet of the problem with little more than the bare remark (1939) that "the universe is a density dependent factor." In so doing, I think he deprives his theory of fullness.

Thompson regards his explanation of natural control as basically philosophical or even metaphysical. His theory is certainly subtle and elusive, as anyone trying to summarize it in a few sentences will soon discover. The following is my own attempt: In any organism's area of distribution, environmental conditions differ from point to point, and the differences vary in time. The environment, including its biotic components, varies primarily because of the ceaseless natural fluctuations of physical factors, but the organism itself also affects the environment. Natural control is the inevitable result of the organism having to live in an environment which varies continually in space and time between favourability and unfavourability with respect to the specific limitations of the organism. Where and when the organism meets favourable conditions its numbers increase, but these conditions never endure long enough for unlimited increase; nor do unfavourable conditions endure long enough for decrease of numbers to zero—except in places that are in any case unsuitable for the organism.

I am not satisfied with that summary but it is the best I can achieve in four sentences. The very elusiveness of Thompson's theory may well be the quintessence of the ultimate truth. Personally I believe his theory to be a large part of the truth, or better, the truth less fully elaborated than it might be because he did not explore the idea of density dependent factors thoroughly. But elusiveness is uncomfortable, hence Thompson has been largely ignored in favour of Nicholson with his simple, easily-grasped concept of control by density dependent factors.

The Theory of Nicholson

Nicholson's theory was first published in 1933. Most people have acquiesced in it, as is quite apparent in the literature. Nicholson has, of course, had a few critics (notably W. R. Thompson, 1939) but has apparently seen nothing of value in their criticism. At all events it has not deterred him from reiterating his theory, unchanged in essential substance, again and again in print (1937, 1947,

1954a, 1954b; and, with Bailey, 1935). His latest exposition (1954b) contains an astonishing section entitled "*The Place of Thought in Research*", prefacing his criticism of other population theories. Here is a sample paragraph:

". . . . A necessary condition for investigation is a continual interplay between thought and observation or experimentation, which leads eventually to understanding. In any sound investigation, thought must occupy a central and dominating position. It must be honest and accurate, and disciplined in the highest degree. It must precede and follow each active step in observation and experiment; and when an understanding of the immediate problem has been achieved, the discipline of thought must be studiously maintained, for much confusion has been caused in biology by extrapolating sound conclusions to fields in which the basic considerations upon which they are based do not apply."

He does not say who is guilty of misguided extrapolation.

In three sentences of his own words (1933), the essence of Nicholson's theory of natural control is this:

"Populations must be in a state of balance with their environments (p. 176). For the production of balance, it is essential that a controlling factor should act more severely against an average individual when the density of animals is high, and less severely when the density is low (p. 135). [That is,] it is essential that the action of a controlling factor should be governed by the density of the population controlled, and competition seems to be the only factor that can be governed in this way . . ., generally competition between animals when seeking the things they require for existence, or competition between natural enemies that hunt for them (p. 176)."

Now a factor "governed [in its action] by the density of the population" is more neatly described as "density dependent" (following Smith, 1935), and a factor not so governed (Nicholson specifies climate) as "density independent". Further, if competition between its natural enemies can control a population, these enemies can be named as agents of control (as indeed Nicholson himself does). Thus Nicholson's disciples, accepting the balance concept, reasonably interpreted his theory as having two main tenets (see Varley, 1947; Elton, 1949; Lack, 1955): (1) that the environment is comprised of density dependent and density independent factors; (2) that controlling factors must be density dependent, and the chief of these are (a) direct competition for resources or space, (b) parasites, (c) predators and (d) pathogens.

Smith's definition (1935, p. 889) of a density dependent factor (which he attributes to Howard & Fiske, 1911) was a factor "destroying a percentage which increased when the numbers of the host increased." Smith indicated that there might be anomalies in the generally accepted classification of factors with respect to density dependence and independence, e.g. he said that "under certain conditions it [climate] is capable of acting as a density dependent factor." Later writers have discussed the difficulty raised by Smith (e.g. Solomon 1949; Allee *et al.*, 1949; Cole, 1950). Nicholson obviously has this in mind when he states in his latest exposition (1954b) that the term density dependent factor "appears to have given rise to some confusion" and the term "density independent factor is still less apt" (pp. 16 & 17). He therefore classifies requisites [factors] in a new way (see Diagram 1). It might be asked why he omits yet another class, namely, *unresponsive* density disturbing factors. The point for us, however, is that among all the different classes he has now created, Nicholson holds that only the "density governing factors" are responsible for natural control. And he ends by saying (p. 17) of the term "density governing factor" that "its meaning is precisely that of 'density dependent factor' according to definition (Smith, 1935)." Hence "density governing" just means density dependent in Smith's sense, and therefore all factors which are not density governing must be density independent

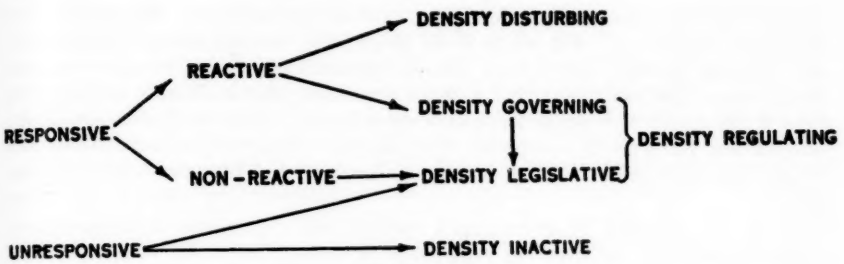

DIAGRAM 1

Fig. 1. Classification of requisites and of their properties in relation to their response to density change and to the influence they have on population density.

because there is no other alternative. Thus Nicholson (1954b) confirms tenet No. (1) of his disciples (see above). Further, he says (1954b, p. 10):

"The mechanism of density governance is almost always intraspecific competition, either amongst the animals for a critically important requisite, or amongst natural enemies for which the animals concerned are requisites."

Thus he also confirms tenet No. (2). In short Nicholson's disciples interpreted him correctly and his theory is unchanged.

Before going on to enquire into Nicholson's theory, yet another quotation from his 1933 paper (p. 144) is needed, viz.

"Further increase of a population is prevented when all the surplus animals are destroyed, or when the animals are prevented from producing any surplus. When this happens the animals are clearly in a state of stationary balance with their environments, and maintain their population densities unchanged from generation to generation under constant conditions. This will be referred to as the *steady state*, and the densities of the animals when at this position of balance as their *steady densities* under the given conditions."

These concepts are necessary to Nicholson's theory, but, of course, the steady state and steady density never occur in Nature!

On the basis of his theory, and with the help of a mathematician (Bailey), Nicholson examined *on paper* the idea of animals searching their habitat, i.e., competing for the things they require, and so developed some equations representing hypothetical parasite-host situations (1933; with Bailey, 1935; the equations were not expressed algebraically in the first paper). In the cases of interaction between host and specific parasite(s) with or without hyperparasites (see Figs. 6 & 7, 1933, and Figs. 10-13, 1935), these equations plainly resulted not in control but in speedy extinction of the populations! This uncomfortable fact was explained away to Nicholson's satisfaction (if not ours) by making untested assumptions about the behaviour and spatial distribution of individuals in the populations (see pp. 161-163, 1933 and pp. 589-590, 1935).

The Nicholson-Bailey equations should not, of course, be taken seriously in the sense that they actually show or predict what is occurring or will occur in Nature. The mathematics merely demonstrate what must result from the particular premises Nicholson made. The main premises were that animals have constant average properties from generation to generation (e.g., constant reproductive and searching powers) and live in an unvarying environment (i.e., everything constant except the population numbers). It is doubtful if constancy in average *potential* reproductive power is a generalisation applicable to insects. In many the size (weight) of the pupa determines the number of eggs formed.

and the average size varies from generation to generation. Size may affect searching power too. But there is no doubt that average *actual* reproductive and searching powers vary widely between generations because of environmental effects other than enemies. Nor is there any doubt that in Nature the environment is not constant from generation to generation. Thus the Nicholson-Bailey premises are not at all in accordance with Nature. They are in fact very drastic simplifying assumptions. They had to be because, as Thompson (1939) points out,

"there is . . . no way of developing a method that can reduce to a manageable [mathematical] form the appalling complexity of natural factors or smooth out their unpredictable irregularities."

The truth of this should be obvious. Even in the relatively very simple controlled conditions of a laboratory *Tribolium* culture, predictive equations are extremely complex. Stanley (1934) needed at least 88 symbols representing 14 factors to express the number of eggs expected to be present when hatching began. Despite all this, Nicholson seems to think that the equations support if not indeed prove his theory of natural control. Thus he claims (1933, p. 176) that

"Detailed investigation of the question of competition between searching animals shows that . . . there is for each species a particular density, referred to as the 'steady density', at which balance exists. . . . Competition always *tends* to cause animals to reach and to maintain their steady densities".

The "detailed investigation" was in fact nothing more than a mathematical exercise using hypothetical animals with constant properties in hypothetical constant environments.

Given their premises, the Nicholson-Bailey equations will, of course, predict correctly. But since nothing like their premises exists in Nature, it would seem naive to appeal to Nature for agreement with the predictions of these equations. Nevertheless this appeal has been made.

Varley (1947) claims (p. 140) to have made the first attempt in the field to confirm Nicholson's theory, or, as he says, its basic assumptions—which amounts to the same thing. So far he seems to be the only one who has deliberately tried to do so. He set himself the problem:

"What factors control the population density of the knapweed gall-fly in nature, and how do they operate?".

And he claimed (p. 182):

"A solution is found by the application of Nicholson & Bailey's theory of 'balance of animal populations' to the results of a detailed census of a series of 92 square metre plots from an area near Cambridge over a period of two years."

Andrewartha & Birch (1954, pp. 443-447) have rejected his claim on general logical and statistical grounds. I think the case for rejection is even clearer when the particulars of Varley's actual procedure are examined.

Varley answered the first part of his problem (what factors control?) in this way: First, he asserted (p. 174) that

"controlling factors must be density-dependent";

then, on that basis, he decided (p. 175) that

"the three factors which appear to have the right properties are the density-dependent early larval mortality, and the two common chalcid parasites, *Eurytoma curta* and *Habrocytus trypetae,* which act as delayed density-dependent factors";

and finally, he argued (pp. 175-180) that

"*E. curta* was the factor primarily responsible for the control of the population density of the knapweed gall-fly" (pp. 180-181).

Now, in the 1935-36 generation (the only complete generation—see Varley's Table 8), a very large part of larval mortality in the gall-fly, (37.1+3.0+30.8+1.8)/184.7 or 40%, was lumped under three vague heads: "died before forming galls", "died due to unknown causes" and "winter disappearance". That is, Varley could not identify, far less specify the action mechanism of, all the individual factors affecting the gall-fly population. This reduces his decision, as to which factors were likely to be controlling, to nothing more than a guess based on incomplete knowledge of the ecological circumstances. Moreover, statistically, the data do not even support the idea that the three factors favoured by him were in fact density dependent (see Milne in Andrewartha & Birch, 1954, pp. 445-447; and see also Varley's second thoughts in Finney & Varley, 1955, which were prompted by Milne though this was not acknowledged by Varley). But most important of all, in choosing these three factors *simply because of their alleged density dependence*[3], Varley nullified his claim to be attempting a confirmation of Nicholson's theory—for the basic assumption of the theory is that controlling factors must be density dependent. Varley neither tested Nicholson's theory nor did he solve satisfactorily the problem of what controls the gall-fly in Nature.

Having said that, it may at first sight seem superfluous to proceed to a consideration of Varley's answer to the second part of his problem: how do the controlling factors operate? However, because of a seeming agreement between the field data and Nicholson's theory, quite a number of ecologists believe that Varley correctly answered the second part (and this would mean that he had guessed rightly in the first part!). Two of the more important instances of this belief must suffice. In their text book of ecology (1949), Allee *et al.* state (pp. 385-6) that Varley's paper shows "good agreement with predictions expected from application of the Nicholson-Bailey equations"; they do not specify the predictions. In his review of population ecology (1949), MacFadyen is more explicit; he says (pp. 538-9) that "the steady densities of host and parasite were estimated and shown to conform in a most remarkable way with conditions found in nature." These authors are referring to the results of a mathematical exercise set out in pp. 176-179 and Table 14 of Varley's paper and his conclusions therefrom in the second column of p. 179 and the first two paragraphs of p. 180.

It is obviously rather important that the facts of Varley's mathematical exercise should be laid bare.

Table 1 shows the relevant excerpt from Varley's Table 14. He says (p. 180, col. 1) that calculated values for steady densities etc. (row (3), Theoretical, in Table 1) are in "striking agreement" with the census data (1935, 1936); thus, "with 92% non-specific mortality acting with *E. curta* all the calculated[4] figures are between the census figures for the 2 years", h being between h′ & h″, u_1 between u'_1 & u''_1, and so on. This, then, is the solution to his problem "by the application of Nicholson & Bailey's theory". Apparently we are expected to believe that Nicholson is vindicated and *E. curta* controls the gall-fly because in 1935 and 1936 the field densities of those insects straddled theoretical "steady densities" based on the simplifying assumptions of Nicholson. Those who believe this have not followed the mathematical exercise step by step.

The theoretical values were obtained by employing averages of the field data for the two years in several equations: the Nicholson-Bailey equation for the "area of discovery" of a parasite (in a form written by Varley), and, partly

[3]In a letter dated 23/4/52 to A. Milne, G. C. Varley confirmed that this was in fact the sole basis of his choice.

[4]For some occult reason, in his calculations, Varley uses sometimes 1.9, 1.5 & 42 (as in Table 1) and sometimes 2.0, 1.66 and 45.5 for p′, p″ and Q′ respectively. This irritating fact must be borne in mind when following his calculations.

TABLE 1

Excerpt from Table 14 of Varley (1947) entitled: "The theoretical effect of different types of mortality factors on the balance between the gall-fly *Urophora jaceana* and its chalcid parasite *Eurytoma curta*." (Note: The values u′ and u″, mentioned in the text, can be obtained by appropriate manipulation of u′, and Q′ and u″, and Q″, or direct from Varley's Table 8.)

Theoretical. Non-specific mortality acting on gall-flies and *Eurytoma* after its attack.	Steady density of the gall-fly		Steady density of adult *Eurytoma curta*	Percentage of gall-fly larvae parasitized
	Adults per sq. m.	Available larvae		
(1) 50% mortality (x = 0.5)	1.1	20	8.8	89
(2) 90% mortality (x = 0.1)	2.9	53	2.4	45
(3) 92% mortality (x = 0.08)	3.3 (h)	60 (u_1)	1.5 (p)	31 (Q)
(4) Over 94.5 mortality (x < 0.055)	0.0	0	0.0	–
Census data for comparison				
1935	6.9 (h′)	147 (u'_1)	1.9 (p′)	42 (Q′)
1936	2.0 (h″)	28 (u''_1)	1.5 (p″)	27 (Q″)

derived from it, some equations apparently invented by Varley to depict the "steady state" of Nicholson. (In passing, it should be noted that this use of averages might oblige the theoretical values to be somewhere between the field values for 1935 and 1936!). All the simplifying assumptions of Nicholson are taken as granted in operating these equations. Thus there is a fixed multiplying power for the gall-fly (18), a fixed "area of discovery" (0.25 sq. m.) for *E. curta*, and a fixed environmental effect on both insects (final choice: 92% mortality). With respect to environmental effect, Varley premises (p. 179, col. 1) that after parasitization the fractions of the two populations surviving to adulthood are the same in gall-fly and parasite. Moreover, his argument (in the same col.) clearly shows an extension of this assumption (not explicitly stated), namely, that there is no differential mortality in the two populations *after* adulthood is reached and *before* oviposition is completed by the gall-flies and parasitization completed by the *E. curta* (when the gall-fly eggs have become second larval instars). In short, apart from the action of *E. curta* on the gall-fly, the total effect of the entire environmental complex is to kill the same proportion of both populations in each succeeding generation! Despite this ruthlessly unnatural assumption, Varley contrived to demonstrate "striking agreement" between field data and theory. The "agreement", however, is an unwitting artefact, a figment of averages, an unjustified 92% mortality factor, and failure to take sampling error into account.

Let us study first the key theoretical value p, on which the other theoretical values h, u_1 and Q all depend. Varley starts with the Nicholson-Bailey equation for the "area of discovery", a, of a parasite which, he says, can be given in the form

$$a = \frac{2.3}{p} \log \frac{u_1}{u} \qquad (1)$$

"where . . . . p is the population density of adult parasites and u_1 and u the population density of host larvae before and after parasitization" (p. 176). Suppose you insert the average field values of p and u_1/u in this equation and solve

for a. If now you insert the new-found value of a and the average field value of u_1/u in the equation and solve for p, you will not be surprised at getting the average field value of p back again. Varley did not do this, but he did something very like it. To find the "steady density" p of Table 1, he constructed the equation

$$p = \frac{2.3}{a} \log Fx \qquad (2)$$

where a is to have the average value 0.25, calculated from equation (1); F, "the natural rate of increase of the gall-fly", is to have the average value 18 (for calculation see later); and x is a *hypothetical* fraction representing the proportion, both of unparasitized gall-flies and of parasites, surviving to adulthood after the parasitization (e.g. 92% mortality gives 8% surviving or $x = 0.08$, see Table 1). Equations (1) and (2) are identical except for the logarithmic term. Obviously, if Fx equals the average of u_1/u, then on solving equation (2) for p, the result must be the average field value for p, i.e. $(p' + p'')/2$ or $(1.9 + 1.5)/2 = 1.7$. Similarly, Fx might differ from u_1/u to the extent that equation (2) will yield $p = 1.5$ which is just included in the range 1.5 — 1.9 covered by the field values in the two years. Now the value of F is fixed at 18. But Varley unwittingly arranges that Fx will differ from u_1/u to the extent of giving $p = 1.5$, by the simple expedient of assigning to x the *hypothetical* value of 0.08. Thus one quarter of the evidence for "striking agreement" is worthless.

Having arranged for p to be in agreement, Varley now inserts it in another equation which he has constructed:

$$h = p/(Fx - 1),$$

wherein we meet the same F and x again. This gives a value of h which is between h′ and h″. Here the agreement emerges from the manipulation of a previously engineered agreement together with half the ingredients of the latter.

Varley now uses h in the equation

$$u_1 = Fh,$$

where F turns up once again. This gives u_1 between u'_1 and u''_1, another agreement. But F was calculated as the average of u'_1/h' and u''_1/h''. Hence if h is between h′ and h″ in value, u_1 is *obliged* to be between u'_1 and u''_1 when it is derived from Fh. That is, another quarter of the evidence for "striking agreement" is quite worthless.

Having arranged for p and u_1 to be in agreement, Varley now uses them to find Q (the percentage of gall-fly larvae parasitized) in the equation

$$Q = 100p/u_1x$$

wherein the familiar x reappears. Needless to say, Q comes between Q′ and Q″.

Obviously, the evidence for "striking agreement" between theoretical "steady densities" and field census data is absurd because half of it was unwittingly "manufactured" and the remaining half is inextricably involved in that "manufacture".

From Varley's Tables 8 and 9, after parasitization by *Eurytoma*, the fraction x surviving in Nature was 0.2 (i.e. 80% mortality) in 1934-35 and 0.03 (i.e. 97% mortality) in 1935-36, the average for the two years being 0.12. Why then did he choose the hypothetical fraction 0.08 on which to base his judgment as to whether there was striking agreement between theory and Nature? To be consistent, he ought to have used the average field value of x, i.e. 0.12, just as he took average field values (p, u_1/u, a & F, etc.) in all other aspects of his theoretical calculations. But if he had been consistent he would have found no "striking agreement", for, with $x = 0.12$, p and Q are respectively 3.1 and 54.

The fact is that among all the possible values of x (rounded to two decimal places) only two, 0.08 and 0.09, do give agreement (the latter value of x resulting in 3.1, 56, 1.9 & 38 for h, u_1, p & Q respectively). Hence even Nature, let alone Varley, had practically no choice in the matter if Nicholson's theory were to be vindicated! Actually, Varley ignores the 1934-35 field data for x and says only (p. 180):

"This correspondence between the calculated steady densities and the census data has been achieved by giving the non-specific mortality a fixed value of 92%. *Doubtless the mean figure for this mortality must be less than 96%*[5], which was the estimate for 1935-36, since with an 18-fold natural rate of increase this would eventually cause extinction of both gall-fly and its parasites."

The italicised phrase in that quotation is the one and only appeal to sampling error. This introduces another reason for judging Varley's mathematical exercise to be utterly mistaken.

The census values given in Varley's Tables 8-14 are all means of samples (or derived from simple arithmetical manipulations of such means) and therefore have sampling errors attached to them. Varley does not give all the sampling errors, and some that he gives are underestimated (see e.g. by Milne in Andrewartha & Birch, 1954, p. 445). But let us accept, without question, what he does give. There are sampling errors for all the census data in Table 1. For example, h′, u'_1, & p′ were estimated as 6.9 ± 1.6, 147.6 ± 21.5 & 1.9 ± 0.65 per sq. m. respectively. Now an estimate such as a mean of 6.9 ± 1.6 from a sample of 10 sq. m. (p. 146) signifies no more than this: there is a strong chance (19 to 1) that the true mean of the population does not lie outside the limits 3.3 and 10.5 per sq. m., i.e., that the population mean is somewhere–*anywhere*–between 3.3 and 10.5. It certainly does not signify that the population mean is actually 6.9. Similarly, 147.6 ± 21.5 signifies a population mean not 147 but anywhere between 103 and 192 per sq. m. Again, $147/6.9 = 21$ is not F′, as Varley would have us believe. Taking the sampling errors into account with 20 degrees of freedom (which favours Varley), the 5% fiducial limits (see Finney, 1950) of F′ are 12.5 and 43.4. This and the like calculation for F″ do not lead to the hard figure 18 for the average natural rate of increase, F. But the statistical weaknesses and misapprehensions need not be laboured further. Sufficient has been said to make this point: because of the relatively large sampling errors, the unqualified sample means used by Varley in Tables 8-14 are untrustworthy as depicting average population characteristics in the field. Indeed the true population characteristics were almost certainly very different, particularly in their relations to one another.

Taking sampling error into account would not have improved matters for Varley to any significant extent since the estimates were too imprecise to serve his purpose. And his purpose was certainly not served by his procedure in general. As noted at the outset, the "striking agreement" was an unconscious artefact. The Nicholson School might well heed Thompson's further remarks (1939) anent mathematical models:

". . . . if the situation in nature corresponded exactly to the mathematical equation, the laws inherent in the equation would be the laws of nature. . . . . But conditions in nature clearly do not reproduce the conditions in the equations . . . . and it is useless and worse than useless to pretend that they do, because the investigator labouring under this delusion may be tempted to force the facts into a mould that will not fit them or may try to find the facts, not in nature, but in the mathematical representation of nature that he himself has constructed. This is not to say that the mathematical theories of populations are useless. They enable us to see clearly how one quantity varies in function of others, under certain conditions. They may suggest and have

[5]Actually 97%, see before.

already suggested experimental investigations and field studies from which very valuable information is derived. But they . . . . are not in any degree a substitute for the investigation of nature."

Thompson was one of the first to construct and use advanced mathematical models; but he was also the first to point out their limitations. I think it would be fair to say that Nicholson himself has caused confusion by misguided extrapolation from the realm of mathematics.

Nicholson's theory of 1933 has never been properly tested, far less confirmed, in the field. In my opinion, his theory is inadequate and very largely wrong, for the following reasons.

For the moment let us accept the epithet "density dependent" as a precise, i.e., mathematical, description of the action of competition, predators, parasites and pathogens. These factors function by hindering the reproductive fulfilment of individuals or by removing or killing individuals. Thus, if they act at all, no matter how strongly or feebly, these factors are *always* positively contributing to *decrease* of population. This ought to make us wary of the proposition that density dependent factors control *fall* of numbers in Nature. Of course, by definition, their action becomes less and less severe as density falls. But progressive withdrawal of one kind of downward pressure will not necessarily render another kind ineffective. If the density independent environment persisted in removing any number of individuals, so that the total disposed of by all factors was more than could be replaced, then numbers would ultimately reach zero despite density dependent factors. I saw this happen to a Tipulid population in a field I was studying during last year's (1955) unusual drought in Britain. In other words, numbers can not stop falling unless the density independent environment is or becomes favourable for that purpose. The ultimate control of fall in numbers rests therefore with the density independent factors.

With rising numbers, the case is different. Here the density dependent factors are not passively withdrawing their aid to the prevailing trend in density. They are actively increasing their opposition to the trend. Accordingly, the idea of density dependent control of rising numbers appears, on the surface, to be reasonable. Nevertheless, Nicholson's theory seems to be largely wrong even in respect to control of increase in numbers. Consider the following sentence in Thompson's earliest statement of his own theory (1929):

"The vast majority of parasites, predators and pathogenic organisms require for their continued existence and propagation, not merely the presence of certain hosts, but also a certain definite complex of environmental conditions *quite independent of the host.*"

This contains the germ of the most cogent objection to the greater part of Nicholson's theory. But Thompson did not develop it in the way I thought would be most effective (see below). And Nicholson has apparently ignored its implications.

Mathematically, it can readily be shown (and has been in several mathematical models) that a *perfectly* density dependent factor would indeed control increase in numbers of a species. Perfection here means an *exact* linear (or curvilinear) relationship between increasing action of the factor and increasing density of the species. But competing species, parasites, predators and pathogens are at best *imperfectly* density dependent in action. Therefore they can not *by themselves* do the controlling. This may be illustrated by reference to parasitic action. For perfectly density dependent action, the population number and/or average individual effectiveness of the parasite would require to be determined *solely* by the density of the host. But if ecological research has shown one thing more clearly

than all else, it is surely the fact that no organism's numbers, nor its functioning, are determined *wholly* by *one* circumstance. Numbers of an organism at any moment are the result of action of a complex of factors. Nicholson's writings show that he appreciates this fact so far as the host is concerned. But he apparently does not appreciate its implications in the case of the parasite. The parasite is also subject to a complex of factors, which, being different from the host's complex, does not have parallel effect. Whatever response the parasite population might make to changes in host numbers is inevitably modified by other factors (1) peculiar to the parasite itself and (2) common to itself and host but affecting each to a different degree. That is, the parasite can not be expected to adjust its numbers, or its intensity of action, *exactly* to the host's density, and indeed no field data have yet shown that it does so. In short, the parasite is not free to act in a perfectly density dependent manner; and so it can not control the host indefinitely. This principle obviously applies to competing species, predators and pathogens as well as parasites.

Some people hold that there is abundant evidence, of one species controlling another, in the annals of "biological control".

Let us deal first with the deliberate introduction of parasite or predator. The great majority of attempts of this kind have failed with insect pests (Taylor, 1955). From our point of view, cases where utter extinction of the pest has occurred must also be deemed failures since extinction is the antithesis of control. On the other hand, there have been a few undoubted successes, such as the famous case of the ladybird (predator) and the cottony-cushion-scale (pest). The successes, however, are not necessarily cases of one animal being controlled, *in the correct sense*, by another. The evidence says only that control occurs at a lower (economic) level after the introduction of the parasite or predator. It does not say that there was no control, at a higher (uneconomic) level, prior to the introduction. Nor does it say that the introduced parasite or predator is *alone* controlling or could *alone* control the pest at the economic or any other level. In fact, the only objective conclusion from the evidence is the obvious and expected one: the successful addition of a lethal factor to existing lethal or hindering factors results in general reduction of numbers, i.e. a lowering of the average level at which control occurs.

Biological control work has *not* furnished incontrovertible evidence that any one species can *alone* control another in Nature. Nor is there any stringent evidence that the concerted action of several species can alone control another species, i.e. that the sum of several imperfections amounts to perfection. Many biological control workers would disagree here. The outlook of the Riverside School (California), for example, is typical of workers attempting to evaluate the rôle of natural enemies in control.

The Riverside School has published a long series of papers including somewhat artificial laboratory experiments on simple parasite-host situations, field observation on natural enemies of pests, and ingenious field experiment on the collective effectiveness of those enemies. For present purposes, five of these papers cover their findings and views adequately (DeBach, with and without collaborators, 1949, 1951a & b, 1955a & b). The ecological analyses are exceedingly flimsy and incomplete (compare the considerable effort of Varley which was nevertheless inadequate); indeed, the overriding impression to the reader is that almost all pest individuals succumb either to enemies (i.e. other insect species), old age or chemicals. Sampling methods are questionable (non-random and open to unwitting bias). Numerical data are almost invariably given in the form

of simple means or totals from samples; thus there is no way of checking the significance of differences nor, if likely to be real, the probable magnitude of these differences (fiducial limits). It can not be over-emphasized that conclusions based on simple means (or totals) of samples may justifiably be doubted. All text books on statistical method make this clear. As an example, Milne (1943, p. 243) pointed out a case in his own work where a mean of 59.6 was not significantly different from a mean of 29.6. In the single instance where the five Riverside papers give the complete sample data in detail (1955a, Table 1), neither the population densities ($P = 0.8 - 0.9$) nor the degrees of leaf and twig damage ($P = 0.8$) were significantly different in treated and untreated lemon tree branches. Thus the conclusions in this case were unjustified.

Study of the five papers mentioned above shows the following. The Riverside School believes that enemies are responsible for controlling citrus pests wherever natural control occurs. They mean, of course, control at an economic level. Where such control does not occur, they blame other factors (usually abiotic) for interfering with the functioning of the enemies. They admit briefly that "meteorological factors may at times depress" host (prey) populations, but hold (1951a) that "such factors are density-independent, hence generally are nonregulatory as far as balance is concerned and cannot, of course be depended upon [for control]." They also admit once that reductions in host (prey) populations are "caused by unknown factors." They never mention bird predation.

Their belief that enemies are responsible for control has apparently two bases. The first is that graphs of enemy and host (prey) numbers in the field rise and fall together through the year. The second is that when enemies are excluded experimentally in the field, numbers of the host (prey) rise "much" higher through the year than when enemies are not excluded. But none of this is proof of responsibility for control. To a certain extent the numbers of any enemy would be expected to rise and fall with its food supply. And naturally, the numbers of the host (prey) are bound to rise higher if the lethal factors are reduced. Only the demonstration of perfect density dependence of enemy action would give the required proof of responsibility. On this question their Tables 3 & 4 (1949) seem to be typical of their data. In the percentages parasitized, there is little more than a weak suggestion of a rather imperfect density dependence which would probably be even weaker if sampling variance were taken into account. As regards relative numbers of predators and prey, it must be pointed out that the simple comparison of their population numbers is not enough; only the proportions *actually killed* by the predators at different densities of prey can show whether or not density dependence exists. The Riverside work shows no more than the fact that in some circumstances enemies may account for large numbers of a pest insect. In so doing, enemies will help to determine the average level at which control occurs. The Riverside work certainly does not show that enemies are in any circumstance alone responsible for control.[6]

In no case has it yet been proved that several different kinds of enemy, acting in concert, can control an insect species at economic levels (or any other levels). Significantly, on the other hand, there is abundant evidence that they

[6]Following up some discussion in Montreal, Dr. DeBach writes (letter 26/9/56): "Briefly, my position is that we have proven that certain natural enemies are capable of maintaining the host population at a level in the field, which otherwise would be much higher if these natural enemies were not present." But they have not investigated whether the lower level would be maintained if the enemies remained and some of the other natural factors were not present. Objectively stated, their claim would be: "we have proven that *an environment* including certain natural enemies is capable of maintaining the host population at a level in the field, which would be much higher if these natural enemies were not present." This contains no unjustifiable implication that the enemies are wholly responsible for control at any level. (See also the second last paragraph of the section on the theory of the present author).

are unable to do so in specific cases. One could fill a book with evidence of devastating outbreaks despite formidable arrays of parasites, predators, and pathogens—sometimes amounting to dozens attacking a single species. A survey of world literature in this respect obviously can not be included here, but it is sufficient to recall the work, on mortality factors for pest insects, of a few men such as Thompson, Massee, Schwerdtfeger, Pickett, Clausen and their associates.

Competing species and the other enemies, singly or in concert, can not control by themselves because they are imperfectly density dependent in action. Nevertheless, any with a sufficiently strong tendency towards density dependence must make an important contribution to control because of this tendency. It might be as well to add that evidence of parasitization or predation does not necessarily mean that either action is density dependent to any significant extent at all. Too much is usually taken for granted here! Published data often show a surprisingly small degree of density dependence (see e.g. from Riverside), or no evidence of it whatever (see e.g. in Varley, 1947), when one takes the trouble (which authors seldom do) to subject the alleged density dependence to statistical tests.

To sum up:—Nicholson holds that natural control of a population of any particular species X is the result of density dependent action arising from some form of competition. It seems clear from the papers of himself and his disciples that there are three forms of competition: (1) the competition of other species for resources or space which are or could be used by X, i.e., interspecific competition; (2) the intraspecific competition of a parasite or predator or pathogen for X; and (3) the intraspecific competition of X itself. I have suggested that no form of competition can control decrease of numbers in Nature unless the density independent environment permits, and that the first two forms can not control increase. So far I have said nothing about the third form of competition in respect to increase nor about Nicholson's concept of population balance. Let us leave these questions until after we have examined the latest of the more substantial theories.

The Theory of Andrewartha & Birch

The theory of Andrewartha & Birch (1954) occupies one short chapter, the 14th, in their book, but it is based on the evidence and argument set out in the preceding thirteen chapters. Therefore a brief description and appreciation of the book is a necessary preliminary.

The book is called "The Distribution and Abundance of Animals", but it deals mainly, though far from exclusively, with insects. Distribution and abundance are the essential expression of the ecology of animals. The fundamental task of the ecologist, or at any rate of the economic ecologist, is to explain the distribution of numbers in space and time. This book turns away from the "community approach" (which has perhaps reached the limit of its usefulness for the present) and tackles the problem in a new and refreshing way. This way is simply to "look at the situation from the point of view of one species at a time." And since the population is made up of individuals, the study radiates outwards from the individual, all else (including other individuals of the same species) being regarded collectively as the environment. This way seems promising. Pursued far enough, it can be as all-embracing as any other approach. Given a representative array of species, a satisfying general theory of distribution and abundance should have a good chance of emerging from a study of their individual ecologies. The authors consider there is already sufficient material of the right quality in the literature. At all events the amount is growing yearly. All

over the world, ecological workers on particular beneficial or pest species are now having a "look at the situation from the point of view of one species". In professing clearly this alternative and possibly more fruitful approach to ecology (which so far has been developing "unsung"), this book probably makes the biggest step forward since Elton's pioneering classic appeared nearly 30 years ago.

After dealing with physiology and behaviour, and analysing environment from a functional and rather economical angle, all with copious examples, the authors go on to empirical illustration (chapter 13) of the mechanisms determining numbers in natural populations. Comparatively few animals have had their ecologies worked out in sufficient detail for this purpose. The cases of 17 different animals are examined. Numbers are shown to be determined in 4 of these animals mainly by weather, in another 5 mainly by "other animals of different kinds", and in the remainder by circumstances connected with "a place in which to live". The point about this chapter is that it illustrates the weakness of the idea that natural control can only be brought about by competition, parasites, predators and pathogens.

In my opinion, the biggest fault with the book is that it adds to the muddle about both the concept of competition and the concept of density dependence. Andrewartha & Birch hold (p. 25) that "the concept of competition is not relevant to the ecological problem [of distribution and abundance]." They brush aside the difficulties of Smith and others (see before) with the conclusion (p. 19) "that 'density independent factors' do not exist", i.e. all factors are density dependent and hence "there is no need to attach special importance to 'density dependent factors'. . ." Since my objection to the theory of Andrewartha & Birch and my own theory on natural control both rest on my understanding of these concepts, this is obviously the stage at which to introduce a brief statement of this understanding.

An animal fulfils itself completely when it lives healthily, realizes its reproductive capacity fully, and dies of old age. An environmental factor is anything in the environment (biotic and abiotic) that helps or hinders the individual in the fulfilment of itself. The interference or competition of other individuals can hinder the fulfilment of any particular individual, therefore competition, when it occurs, is a factor. No one denies the occurrence of competition in Nature. Usually it is mild and/or infrequent. But since it occurs and hinders fulfilment when it occurs, it can not be irrelevant to the problem of natural control, for the latter is a question of what hinders the fulfilment of individuals.

The common belief is that a density independent factor is one which affects a *constant* proportion of the population irrespective of its density (see e.g. Uvarov, 1931, Nicholson, 1933, Smith, 1935, and others up to the present day). Andrewartha & Birch rightly object (p. 18) that there is no evidence of such constancy in the action of any component of environment. But they wrongly jump thence to the conclusion that density independent factors do not exist. One would have thought it hardly necessary to point out that a factor could affect a *varying* proportion and still be density independent. Any factor, whose action varies so that it may affect a larger or smaller proportion of population irrespective of density must be classed as density independent.

There are plenty of examples of such factors, but three must suffice. Browsing animals kill countless insects by swallowing them along with herbage and leaves or by treading on them. This action is entirely independent of the insect density, and therefore is a density independent mortality factor. The predation of some birds on insects is also density independent (see, e.g. in Betts, 1955). The third

example is weather. When Smith said climate (through shelter) can act as a density dependent factor, he must have meant weather because, unlike weather, climate at any place is for all practical purposes constant. The idea that weather can act as Smith suggested is fallacious. Suppose an area with only 100 safe individual shelters from a particular (high) degree of weather severity (but more than 1000 shelters from any lower degree). It follows that 50%, 75% and 90% of 200, 400 and 1000 individuals respectively would perish when such numbers occurred in the area at times of such severity (providing all the safe shelters are filled). These increasing percentages, however, are not evidence of weather acting as a density dependent factor. Population may increase from 200 to 1000 without that particular severity of weather ever occurring. Weather is not governed by density of individuals present. It can be benignly favourable or severely unfavourable (e.g. to mating, oviposition, development or survival, etc.) whether density is high or low. Weather is a very important density independent factor in the life of an insect. Density independent factors undoubtedly exist.

In the literature one often sees food and space referred to as density dependent factors. This belief is also fallacious. Neither food nor space reacts to density according to definition. Indeed as density rises food, and the proportion of space that is suitable, quite often increase due to favourable weather or other circumstances. They certainly define the limit of density at which the population would extinguish itself. But they have no density dependent action of themselves. Their available amounts are merely consumed or filled to a greater or lesser degree. It is not food and space themselves, but the competition for them that is density dependent. This applies equally to food when it is a living animal, i.e. prey or host. Hence I do not agree with Varley's (1953) volte-face, viz.

"great confusion has arisen because . . . many [authors] . . . have assumed that parasites, predators and disease organisms act as density-dependent mortality factors on their hosts or prey whereas . . . it is the population density of host or prey which acts as a density dependent factor on the parasite or predator."

I hold the view that the only factors with any capacity for density dependent reaction to the numbers of animals are the animals themselves. They manifest this reaction by varying the intensity of their intraspecific or interspecific competition for resources external to themselves, and to some extent by varying the intensity of their utilisation of other animals as a means of livelihood.

In my understanding, then: (1) competition is relevant to the problem of natural control; (2) the only factors likely to have any degree of density dependence are animal actions, and all other environmental factors are density independent.

Returning now to Andrewartha & Birch: Though different in some respects, their views on natural control are reminiscent of Thompson's. This is evident throughout chapter 14 but not to any great extent in the bare summary of their theory which runs, in their own words, as follows (pp. 660-661):

"The numbers of animals in a natural population may be limited in three ways: (a) by shortage of material resources, such as food, places in which to make nests, etc.; (b) by inaccessibility of these material resources relative to the animals' capacities for dispersal and searching; and (c) by shortage of time when the rate of increase, r, is positive. Of these three ways, the first is probably the least, and the last is probably the most important in nature. Concerning (c), the fluctuations in the value of r may be caused by weather, predators, or any other component of environment which

influences the rate of increase . . . (r has three constituents: fecundity, speed of development, duration of life)."

Now, in effect, (a) is the same as (b) and both lead to (c) because r can be positive only so long as resources or their accessibility allow. Thus their theory seems to boil down to the one idea expressed in (c) and its qualification. To put it in other words: natural control is a matter of numbers increasing and decreasing just so long as the environment permits (a truism!); environmental conditions fluctuate and the requisite conditions do not endure long enough either for unlimited increase or for decrease to zero; the ruling components of environment in this respect are multifarious and by no means confined to competition, parasites, predators and pathogens. Obviously they are largely agreeing with Thompson.

On the evidence marshalled in their book, it would be difficult to disagree with their theory *so far as it goes*. They could take it no farther because they concluded at the outset that density dependence in a factor has no "special importance" since all factors are density dependent. In this view, it seems to me, they are just as mistaken as the Nicholson School in its assumption that competing species, parasites, predators and pathogens have that perfection of density dependent action necessary for control.

The Theory of the Present Author

Nicholson holds that a population must be in a state of balance with its environment. He suggests that this balance is analogous to that, say, of a tight-rope walker (1954b, p. 23). But the environment is continually changing. No tight-rope walker would be expected to balance on a rope that is continually being moved unpredictably to new positions willynilly in all directions. How then can a population be expected to exist in a state of balance with its environment? I do not believe any natural population is in this state.

As I see it, the environment rules. Of course, to a variable extent, the organisms themselves are partly responsible for the conditions, but that does not alter my proposition. Numbers increase when conditions permit and decrease when conditions so dictate. There is balance, but not between population and environment. The balance is in the environment itself. Through space and time, favourable conditions are balanced by unfavourable conditions in such a way that populations continue to exist, i.e., are controlled. It is the way this world is made. But we want to know the details of the mechanism. My theory might be described as a distillate of elements from Thompson, Nicholson, Andrewartha & Birch, and many others, mingled with my own field experience. Thompson's theory obviously contributes by far the largest element, and indeed my theory might well be described as a modification of Thompson's.

I reject the plurality in the dogma of the Nicholson School. A *perfectly* density dependent factor will control increase of numbers endlessly, but there is only one such factor in Nature for any species. That factor, the ultimate controlling factor for increase, is the competition between its own individuals, i.e. its *own* intraspecific competition. This is the only factor affected solely by numbers and therefore with an unfailingly exact response to numbers. Yet it is a matter not merely of numbers as such, but of numbers in relation to both the organism's needs and environmental capacity at the time. It takes effect from that level of density at which resources (food, space, etc.) begin to be insufficient for the full untrammelled expression of the individual. Above that level its effective response to changes in density is exact and immediate, not delayed. It can control because it has variable material to work on. With its own intraspecific competition a population avoids self-annihilating increase because of the

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constitutional variation of the individuals comprising it: some individuals give way before others (either by emigrating or dying) and thus danger is automatically and immediately lessened. In general, no species in natural circumstances will consume resources over the whole of its range to the extent of all individuals having to die.

However, it is quite plain that in Nature most species, in most places for most of the time, are held fluctuating at population levels where intraspecific competition is relatively insignificant as a check to increase. That is, the ultimate controlling factor for increase is seldom evoked. What then holds numbers so far below the limit of resources for so long if not almost endlessly in so many species of insects? It seems the answer must be: the *combined* action of factors which are density independent and factors which are imperfectly density dependent, *each supplying the lack of the other.* Are we then to regard intraspecific competition as unimportant in the question of control of increase in numbers?

The only really long-term *quantitative* study of insect populations is reported by Schwerdtfeger (1935, 1942). This deals with the pupal or larval density of four forest moths in December at Letzlingen, Germany, and covers the sixty years 1881-1940. If we start at 1891, only one of the species showed any outbreak during the long course of half a century! If we start back at 1881, a second species registers an outbreak. Who knows whether or not the remaining two species would have registered outbreaks had the observation period covered more than sixty years. Undoubtedly the ultimate controlling factor for increase, intraspecific competition, is usually seldom evoked, but it would be rash to claim for any species that it is *never* evoked. If it is evoked at all, no matter how seldom, then, in the long view, it is the all-important factor in preventing extinction from multiplication to the point of collective suicide.

As already indicated in my criticism of Nicholson's theory, the ultimate controlling factors for decrease of numbers are, in my opinion, the density independent factors. For, unless the latter begin at the appropriate time to favour increase instead of decrease, the remnant of individuals left by the imperfectly density dependent factors will perish.

Provided the density independent environment never annihilated, and provided emigration was not precluded when necessary, then, in this theory, a population could remain in being without the help of any imperfectly density dependent factors. Numbers would fluctuate between, and occasionally to, a lower limit set by the most unfavourable density independent conditions and an upper limit set by intraspecific competition in accordance with the most favourable density independent conditions. It can be inferred [from the known influence of weather, with its irregular pattern of variation, on insects, and, in particular, from Schwerdtfeger's graphs (1935, 1942) of population densities in forest moths] that the curve of numbers would fluctuate irregularly in time to irregular heights and depths. One effect of adding imperfectly density dependent factors (i.e. competing species, predators, parasites and pathogens) to this system would be a tendency for the upward component of fluctuation to be dampened. There can be no more than a *tendency* to damping, because of the imperfection of the density dependence giving rise to it. Although it could not be relied on to prevent numbers rising to levels necessitating the check of intraspecific competition, this tendency would *help* to make the rise to such levels less frequent. Another effect of the imperfectly density dependent factors would be not a damping but an enhancing of the downward component of fluctuation. This

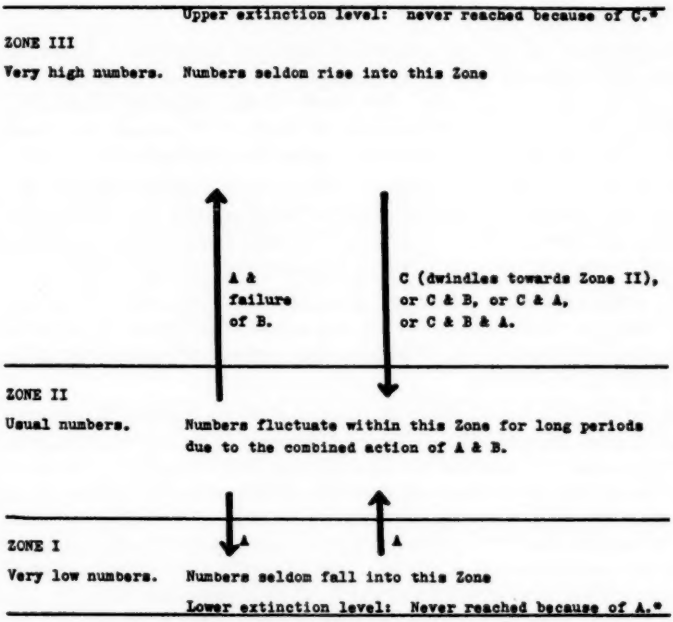
Upper extinction level: never reached because of C.*
ZONE III
Very high numbers. Numbers seldom rise into this Zone
A & failure of B.
C (dwindles towards Zone II), or C & B, or C & A, or C & B & A.
ZONE II
Usual numbers.
Numbers fluctuate within this Zone for long periods due to the combined action of A & B.
ZONE I
A
A
Very low numbers.
Numbers seldom fall into this Zone
Lower extinction level: Never reached because of A.*

DIAGRAM 2

Illustration of Theory of Natural Control of a Population

A = Density Independent Factors (total effect).

B = Imperfectly Density Dependent Factors.

C = The One Perfectly Density Dependent Factor (intraspecific competition).

Arrows indicate departure and return of numbers from and to the usual level, Zone II. Factors causing departure and return are shown beside the arrows.

* NEVER, if the area is not too small or if emigration/immigration is not precluded.

follows because parasites, predators and pathogens must always remove some individuals from the host (prey) population in order to permit the continued existence of their own populations. The damping of the upward component and the enhancing of the downward will offset each other to some extent. I should only be guessing if I suggested that the net effect would be either greater or lesser stability, i.e. a smaller or larger average range of fluctuation. But undoubtedly the average level of the curve of numbers would be lowered. Here it should be noted that while the introduced factors cause the *lowering* of the average, they are only partly responsible for the average itself since the latter results from the action of both introduced and previously existing factors.

There is not space here to expand my theory in greater detail. It is summarized in Diagram 2. I might add that I was unaware of Glen's paper (1954), on "Factors that affect insect abundance", until after the Montreal Conference in 1956. Considering the popularity of Nicholson's theory, it was interesting to find that Glen's views and mine agree at several points. My theory may or may not be acceptable as a small advance on previous ideas on the mechanism of natural control. But I shall be well content if my paper does no more than help to put an end to the stagnation of thought and research engendered by wide and uncritical acceptance of Nicholson's facile but mistaken dogma.

Summary

The problem of natural control of numbers is defined. Three theories are described and examined: the prevailing theory (that of Nicholson, 1933, which is similar to Smith's, 1935), and the most useful opposing theories (those of Thompson, 1929, and of Andrewartha & Birch, 1954, which are similar to one another). The author's own theory is given in conclusion.

The main objection to Nicholson's theory is that competing species, parasites, predators and pathogens can not control because they are *imperfectly* density dependent in action. This is at once obvious from simple mathematical and ecological considerations. It is also confirmed by the field evidence.

The main objection to the theories of Thompson and of Andrewartha & Birch is that they either pay too little attention (Thompson) or attach no special importance (Andrewartha & Birch) to the concept of density dependence, and so are deprived of fullness.

Taking the best out of these theories, and in the light of his own experience, the author puts forward the following theory: A *perfectly* density dependent factor or process will control increase of numbers endlessly. There is only one such in Nature for any species and that is competition between its own individuals. This is the ultimate controlling factor for increase. But in Nature, most species, in most places for most of the time, are held fluctuating at population levels where this kind of competition is relatively insignificant. That is, the ultimate controlling factor for increase is seldom evoked. The suggestion therefore must be that control of increase is, for most of the time if not almost endlessly, a matter of the *combined* action of factors which are density independent and factors which are imperfectly density dependent, *each supplying the lack of the other.* The ultimate control of decrease of numbers is brought about by density independent factors.

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An Interesting Attractant for *Priacma serrata* (Lec.), (Cupesidae: Coleoptera)[1]

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On the warm morning of May 27, 1956 at the Trinity Valley field station near Lumby, B.C., some laundry hanging out to dry attracted large numbers of a strange Cerambycid-like beetle. Closer examination showed this insect to be *Priacma serrata* (Lec.) of the family Cupesidae (Fig. 1), an interesting and infrequently collected species.

The family Cupesidae seems to have no economic importance, having only two genera and five species in North America that have been described (Blatchley, 1910). The larvae are reported to live in rotten wood; dissection of some adults collected at this time produced an entirely empty and deflated gut. The females and larvae of the closely related *Micromalthus debilis* Lec. are found in rotting wood in North America and were reported from decaying mine timbers far under ground in Johannesburg.

Little is known about the biology of this family. Most of the papers on Cupesids are taxonomic and there seems to be a controversy about where the family belongs. Some, such as Kolbe and Gahan favour its placement in the Adephaga (Barber & Ellis, 1920). Leconte, Horne and others place it in the Serricornia with the Cucujidae (Barber & Ellis, 1920). Since the male terminalia suggests that it is dyphyletic, Edwards (1953) thought it possible that the forbears of this group branched from the ancestral Coleoptera prior to the divergence of the Adephaga and Polyphaga. It is evidently a very primitive group as the elytra of *Permocupes* are present in the Upper Permian deposits of Karan (Jeannel & Paulian, 1949). This would support the opinion of Edwards as it was during the Permian that the first representatives of the Coleoptera appeared (Ross, 1948). The tarsal formula of *Priacma* being 5, 5, 5, also supports placement in the Adephaga or prior to it. Böving and Craighead (1930) placed the Cupesids in the more primitive Archostemata with the Micromalthidae on the basis that their larvae are so ancient they must be isolated from the beetles as an almost extinct type.

The presence of these insects in large numbers aroused interest and the resulting observations showed the largest numbers to be present on several white articles that had been washed in a solution of domestic bleach containing 5 per cent available chlorine. The following day a series of coloured articles were hung out about 9.00 a.m. Some were left dry, some were dipped in water, and some were dipped in a solution of bleach. Similarly treated sheets of newspaper were added to the experiment and two pans, one containing water and one containing bleach solution, were set out.

The area was checked five times throughout the day. The air temperature and the number of *Priacma* on the articles were recorded at each observation. The first beetle was seen at 9.40 a.m. when the temperature was 52.5°F. At the end of nine hours and 25 minutes 245 beetles had been recorded, nine on the dry articles, nine on the articles treated only with water and in the pan of water, and 227 on articles wet with bleach and in the pan containing bleach solution. The largest number of beetles was observed at 3.20 p.m. when the temperature reached a peak of 75.5°F. Most beetles were recorded in the pan of bleach while two white towels treated with bleach produced the next highest counts.

[1]Contribution No. 342, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

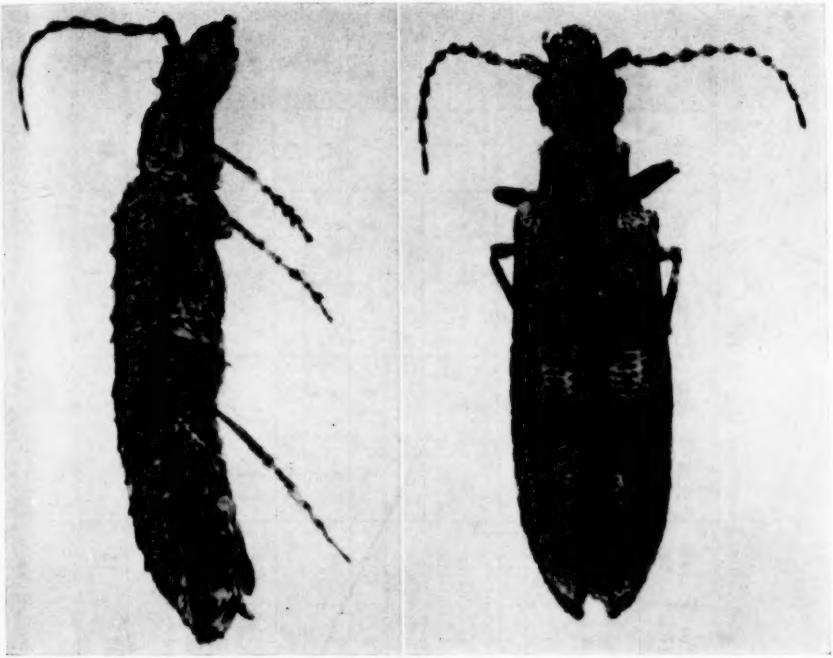

Figure 1. Lateral and dorsal view of male *Priacma serrata* Lec.

The results were so interesting and appeared to be so definite that further tests were planned for the third day. It was decided that colour as well as the other factors should be tested. To do this 9 x 12 inch sheets of coloured, coarse fibre paper were hung by strips of Scotch tape about one inch from string lines and about three inches apart. The Scotch tape reduced the possibility of beetles moving to the sheets from the string.

Two groups of colour classes were set up. Class 1 contained brown, green, and white. Class 2 contained blue, yellow and red. Each colour was tested with the three treatments; wet, dry, and with bleach. Three 18-inch squares of white cotton, one of each treatment, were also set out. To overcome the drying of the coarse paper squares, the water- and bleach-treated sheets were sponged at half-hour intervals half way between the recordings. The temperature and number of beetles present were recorded every half hour from 10.30 a.m. to 4.30 p.m. The results of these counts appear in Tables I and II. Of the 210 beetles observed on the paper squares, 162 were recorded on bleach-treated paper while only 28 were recorded on the dry paper and 20 on the water-treated paper. A similar situation occurred on the cotton squares as can be seen from Table II.

At 9.00 a.m. on the fourth day, the three colours which previously appeared to be most attractive (blue, brown, and white) and representing each of the treatments, were set out on solid objects. One set was placed on a large western cedar, one set on the side of a building and the third on the ground. Counts were made every hour and the totals are recorded in Table III. The pans were

TABLE 1

No. of *Priacma serrata* Occurring on Sheets of Treated Coarse Fibre Paper May 29, 1956.

Time Temp. (F°)		10:30 58	11:00 62	11:30 65	12:00 67	12:30 71	1:00 73	1:30 77	2:00 76	2:30 79	3:00 79	3:30 80	4:00 80	4:30 80	Total
Colour	Category	Number of Beetles													
Brown	Bleach		1	5	5	2		4	1	2	2	3	1		24
Green	Water														
White	Dry	1			1	1									3
Brown	Dry	1	1		1	2									5
Green	Bleach			2	2			1	1				2	1	9
White	Water							1							1
Brown	Water					1						1			2
Green	Dry														
White	Bleach			3	4	10	9	8	7	3	4	5	7	1	61
Blue	Bleach		1	4		2	2	3	3	5	4	4	5	2	35
Yellow	Water				2	3	1				1	1			8
Red	Dry		1	2	3					1			1	1	9
Blue	Dry			3	1	3			2	1					10
Yellow	Bleach	3	2	3	2	4	4		1	1		1	2	3	26
Red	Water					3					1				4
Blue	Water	1			1		1						1	1	5
Yellow	Dry													1	1
Red	Bleach	1			1	2							2	1	7
Totals		7	6	22	23	33	17	17	15	13	12	15	21	11	210

TABLE 2
Number of *Priacma serrata* Occurring on White 18″ Squares of Cotton, May 29, 1956

Time Temp. (F°)	10:30 58	11:00 62	11:30 65	12:00 67	12:30 71	1:00 73	1:30 77	2:00 76	2:30 79	3:00 79	3:30 80	4:00 80	4:30 80	Totals
Category	Number of Beetles													
Dry	1	5	1	0	0	0	1	0	2	0	0	1	0	11
Water	1	5	6	2	6	2	2	4	5	1	4	4	1	43
Bleach	2	4	10	12	16	11	15	22	16	18	16	22	20	184

TABLE 3
Number of *Priacma serrata* Occurring on Treated Sheets of Coarse Fibre Paper, May 30, 1956

Location	Colour	Category	Totals
On Cedar Tree	Brown Blue White	Water Bleach Dry	2
On Building	Brown Blue White	Dry Water Bleach	4
On Ground	Brown Blue White	Bleach Dry Water	1

also set out. The one containing the bleach solution collected 19 Cupesids while the pan containing water failed to collect any. This was the last day of the flight.

It is interesting to note that there was the same mass stimulation to mating as was recorded following their attraction to soap, by Edwards (1951). In recent correspondence Edwards mentioned his failure to attract the beetles to towels dipped in soap, but he was unable to remember whether or not bleach was used in the washing solution which first attracted the beetles. At Trinity Valley, chains of *Priacma* up to nine individuals long were observed in copulatory posture. All beetles so observed were males. In *Micromalthus* no males were found in the decaying timbers but females and paedogenetic larvae were reported in large numbers. (Pringle, 1938).

If these beetles breed or feed in rotting wood, as do their eastern relatives, one would expect them to be at some stage either xylophagus or mycetophagus. If they belong with the Adephaga or Cucujidae one would expect them to be predacious. However, Dethier (1947) lists many attractants for such forms and chlorine is not among them. In fact, chlorine is only considered in connection with repellents. No other insects were attracted to the bleach over the four day period.

Since those four days in May we have been on the lookout for a re-occurrence of this phenomena, but only a few individuals of this strange insect have been seen since.

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Effects of the Food Plant of California Red Scale, *Aonidiella aurantii* (Mask.) on Reproduction of its Hymenopterous Parasites[1]

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Discrepancies in the degree of biological control of insect pests where the food plant species of the host were the only known variants in the environment have been subjects of scattered observations in the literature by Morgan (1910), Compere (1936), Gilmore (1938), and others.

A long period of speculation on the existence of strains of California red scale, *Aonidiella aurantii* (Mask.) immune to attack by parasites culminated in the discovery by Flanders (1939a, 1942a) that the hymenopterous parasite *Habrolepis rouxi* Comp. reproduced satisfactorily on *A. aurantii* on *Citrus* spp. but that very few emerged from the same species of scale on sago palm, *Cycas revoluta* Thunb. This was considered to be the reason for Compere's early failure to bring the hymenopterous parasite, *Comperiella bifasciata* How. from the Orient to California on scale-infested sago palm; Smith (1942) concluded: "Recognition must be given to the possibility that the host plant may confer on the host insect a kind of immunity to parasitization".

More recently, DeBach, Fleschner, and Dietrick (1949) wrote: "Under comparable conditions the red scale on oranges is under better natural control than on lemons. This may be correlated with the activity of the golden chalcid [*Aphytis chrysomphali* Timb.] which seems to work more efficiently on oranges than on lemons, as well as with the probability that red scale increases more rapidly on lemons and therefore attains higher populations before the natural enemies can take over".

In each case cited above, the effects of the food plants of the host upon its parasites were obvious. Environments were identical for the host insect, its food plants, and its parasites, though temperature and humidity changes occurred daily and seasonally.

The objective of the investigations reported below was to demonstrate the effect of several plant species on a single phytophagous insect species, California red scale, and on the development of its parasites.

Equipment and Methods

The experimental work was done in the Division of Biological Control, University of California, Riverside, California, during 1948 and 1949. It was

[1]Based, in part, on a thesis submitted to the University of California in fulfillment of the requirements for the degree of Doctor of Philosophy.

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first attempted in two small, temporary greenhouses of translucent plastic. Because of difficulties encountered in temperature regulation the work was transferred to an air-conditioned, glass greenhouse with automatic temperature and humidity controls. A constant temperature of $80 \pm 1.5°$F. was maintained. Humidistatically controlled water atomizers provided a relative humidity of 55 per cent.

Plant Species Investigated

The following plants were used as experimental hosts of the California red scale: Valencia orange (*Citrus sinensis* Osbeck), Eureka lemon (*C. limon* Burm.), Marsh seedless grapefruit (*C. paradisi* Macf.), yucca (*Yucca filipendula*), sago palm (*Cycas revoluta* Thunb.), and agave (*Agave decipiens* Baker). Nine additional species of known hosts were discarded after initial tests because of severe leaf drop that resulted from scale feeding or because of unsuitable leaf-size or texture. For uniformity of culture all plants were grown under identical soil conditions in five-gallon cans. A layer of sand on the soil surface inhibited the reproduction of a small cecidomyiid that otherwise bred in troublesome numbers. Tubers of the potato, *Solanum tuberosum* L. and stems of the castorbean, *Ricinus communis* L., were utilized during the experiments.

Handling California Red Scale

An ample supply of fresh scale crawlers was provided by mass-production units of the Division of Biological Control, described by Flanders (1947b), making the maintenance of "mother" stocks unnecessary. When needed, a few crawlers were brushed from squares of black cardboard onto the upper surfaces of individual leaves. Upper leaf surfaces were more suitable than stems as they provided broad, flat planes on which several ovipositing parasites could be observed simultaneously. Two or three leaves of each plant were infested with crawlers at five weekly intervals, providing identical host insects for five replicate tests of two species of parasites. Only healthy, plump, well-spaced, female scales were left on the leaves, thus reducing to a minimum the injury to the plants. A few male scales were required, as *Habrolepis rouxi* (Hymenoptera: Encyrtidae), one of the experimental parasites, oviposits only in gravid female scales. Dust that might entangle the antennae of the parasites was removed by means of an artist's brush.

Experimental Parasites

Species investigated.—*Comperiella bifasciata* How. (Hymenoptera: Encyrtidae), *Habrolepis rouxi* Comp. (Hymenoptera: Encyrtidae), *Aphytis chrysomphali* (Mercet) (Hymenoptera: Aphelinidae), and *A. lingnanensis* Comp. (Hymenoptera: Aphelinidae) were used in the experiments reported herein. All four species were imported, mass reared, and studied in considerable detail by the Division of Biological Control, University of California, as reported by Compere (1926, 1936, 1955), Compere and Smith (1927), Flanders (1939a, 1942a, 1943a, 1943b, 1944a, 1944b, 1949a), Smith (1923, 1929, 1942, 1946), and Smith and Flanders (1948, 1949).

Propagation and handling.—The pale, yellow colour and diminutive size of adults of *A. chrysomphali* and *A. lingnanensis* made handling and detailed observations of these species virtually impossible. Experimentation was, therefore, limited to demonstration of their preferences for individual food plants of the host, as described below, using mass releases of adults from production units of the Division of Biological Control as described by Flanders (1951).

Stocks of *C. bifasciata* and *H. rouxi* were maintained on California red scale growing on potato tubers in muslin-covered battery jars. The freshly emerged

adults, during a pre-ovipositional period of 12 hours, were provided with honey only, in hair-line streaks on the jars. This period of isolation from the host scale induced more active oviposition and less host feeding when the parasites contacted the experimental hosts. To facilitate close observation of parasite ovipositions on hosts growing on plants of different heights, an adjustable wooden stand, operated on the principle of a windlass, was constructed to elevate any plant to eye-level. This incorporated an adjustable platform to hold scale-infested leaves in a convenient position for observation and a cellulose acetate shield from which escaped parasites could be retrieved.

Populations of *A. lingnanensis* were distinguished from those of *A. chrysomphali* by pupal markings described by Compere (1955) as the best taxonomic characteristics for separating the species.

Host-food-plant preference.—To demonstrate the preference for particular food plants of the host, 250 fresh adults of each of *A. chrysomphali* and *A. lingnanensis* were released in a temporary, plastic greenhouse containing only two plants each of *Y. filipendula* and *C. revoluta* which were infested with first-, second-, and third-instar California red scale. Additional host-plant preferences of the same two parasite species were shown by 200 adults confined together in small cages each containing grapefruits and potato tubers infested with California red scale; after 21 hours the grapefruits and potatoes were transferred to organdy-covered fruit jars to determine the number of progeny of each parasite species.

Indirect effects of plants upon parasites.—The effects of the six plant species upon the size, sex ratio, life cycle, reproductivity, and longevity of the adults and mortality of the immature stages of *C. bifasciata* and *H. rouxi* were shown by five replicate experiments. Adult parasites were allowed to attack each of the five weekly infestations of scale, described above, as each attained the proper stage for attack, i.e., at weekly intervals. The scales attacked by each parasite species were contained on one or two leaves, a fresh series of leaves being used each week, and all leaves in the five replicates were on the same individual plants.

When adults of *C. bifasciata* and *H. rouxi* were ready for use they were placed individually in gelatin capsules and ejected by sharp raps to the scale-infested leaves. They usually remained on the leaves and began oviposition. Any escapees were attracted by a lamp to a transparent shield. The negatively geotropic *C. bifasciata* and the extremely apprehensive *H. rouxi* required very different handling techniques. Not more than five to eight ovipositing females of these species could be kept under observation simultaneously. Parasitized scales were identified by circular marks of a ball-point pen on the leaves, the date and the parasite species also being recorded on the leaves. Scales containing pre-pupal parasites (indicated by dark brown meconia) were removed and stored in vials to permit accurate emergence records to be made.

In an attempt to determine the effect of the host plant on the sex ratio of the F2 generation of a bisexual, uniparental parasite on a common host plant, groups of three adults of *H. rouxi*, each reared from one of the six host plants, were placed on mated scales on individual potato tubers in separate organdy-covered jars. The F2 emergents were removed and recorded daily.

Results and Discussion

Reaction of Plants to Feeding of Scales

The reaction of the leaves to the toxins injected by California red scale was most evident on the *Citrus* spp., of which the lemon was least injured. Infestations of 15 scales per leaf of Valencia orange and grapefruit resulted in severe

chlorosis and leaf-drop. Leaves of Eureka lemon, however, dropped only when infested with several times this number of scales. Excessive numbers of scales resulted in severe damage and even death to potted *Citrus* spp., with subsequent delays in the experimental work. Concentrations of scales greater than 10 to 15 per square centimetre produced extensive brown, dead areas, on the large, fleshy leaves of agave. Heavier infestations of scales caused no apparent injury in the field, however, where growth was less succulent. Sago palm showed little or no injurious effect from California red scale and its stiff, glossy leaves did not change colour even at the feeding points of the scales. Yucca proved to be a particularly suitable host plant for several reasons: feeding of the scales produced little apparent harmful effect on the leaves in the greenhouse or in nearby gardens; the upper leaves of experimental plants remained entirely free of scale as there was no movement of crawlers up the rough trunk; no loss of scales or of parasites resulted from leaf damage such as occurred on most of the other plants tested; and the broad flat leaves provided satisfactory working surfaces for studies of scales and parasites; when a leaf had been used for one generation of scales it was severed near the trunk, thus removing a possible harbour for extraneous scales.

The excellence of yucca as a host plant of California red scale suggests its use in practical biological control in a manner similar to that suggested by Flanders (1949b) who recommended that the control of black scale, *Saissetia oleae* (Bern.), on *Citrus* spp. be assisted by planting oleander upon which black scale of all stages could thrive at all times, and thus provide a constant supply of hosts for such parasites as *Metaphycus helvolus* Comp. Yucca grows with a minimum of care and would provide a valuable reservoir for parasites of red scale on fruit trees.

Effects of Plants upon California Red Scale

California red scale has been studied in detail by Bliss, Broadbent and Watson (1931), Jones (1936), Yust (1943) and others and is discussed here only as it pertains to the present problem.

Length of life cycle.—California red scale on six different host plants developed from early "crawler" stage to adult stage, from which "crawlers" were emerging, during periods shown in Table I. Those on lemon matured in 46.5 days, or about five per cent less time than those on grapefruit or orange. The

TABLE I

Averages of five replicate tests showing developmental periods in days of *C. bifasciata*, *H. rouxi*, and red scale on six host plants

	Red Scale	*C. bifasciata*		*H. rouxi*
		♂	♀	
Agave	46.0	25.5	26.7	19.2
Yucca	43.0	27.3	28.2	19.5
Lemon	46.5	29.2	29.0	20.4
Sago palm	47.5	28.0	29.3	*
Orange	49.5	28.5	29.8	20.7
Grapefruit	49.0	28.7	30.0	20.0

*No emergents.

TABLE II
Average lengths in millimetres of female parasites and hosts on seven food plants

	Red Scale	*C. bifasciata*	*H. rouxi*
Castor bean	1.49	1.10	1.14
Yucca	1.44	1.04	1.08
Lemon	1.34	.94	.97
Agave	1.31	.88	.96
Grapefruit	1.31	.90	.95
Sago palm	1.30	.86	*
Orange	1.29	.87	.91

*No emergents.

shorter life cycle on lemon has been given as one reason for the occurrence of heavier infestations on lemon than on other *Citrus* spp. in California. The shortest life cycle, as shown in the table, on *Y. filipendula* may account for the encrustations of scale on this plant in gardens in Riverside, California; in spite of these heavy infestations, damage to the plant was never significant. The length of life cycle is presumably a measure of the suitability of the plant species as host.

Size.—California red scale reached a noticeably greater size on yucca than on the other five plant species tested (see Table II). Scales on lemon, being larger than those on the other *Citrus* spp., contain more embryos and thus have greater reproductive capacities. This may be an additional reason for heavy populations that occur on lemon in California.

The castor bean, *Ricinus communis* L., though not used during the experiments because of thrips injury, produced on its stems very large scales with an average diameter of 1.49 mm. as compared with 1.44 mm. on yucca. The parasites produced from these were also above average size.

The sizes of the scales shown in Table II are directly proportional to those of the parasites from the different plants. (For comparison see discussion on adult parasites). This is to be expected as the size of the individual parasite depends largely upon the available food supply.

Morphological characteristics of the scales.—Scales reared on the upper surface of the yucca leaf were plump and regular whereas those reared on the lower surface were invariably distorted in outline and reduced in size. Dr. R. C. Dickson (unpublished notes) believed that these irregularities resulted when the pygidia, during their rotation in the formation of the scale covers, encountered obstructions which were by-passed. The obstructions in this case were corneous protuberances that gave the lower surface of the leaf a texture of coarse sandpaper.

Effects of Plants on Parasites

Host-food-plant preference.—A. chrysomphali and *A. lingnanensis,* liberated *en masse* in a small greenhouse, showed marked differences in preference for hosts living on certain plant species. Of 236 parasite pupae from scale on yucca, the ratio of *A. chrysomphali* to *A. lingnanensis* was 1:3.1 whereas that of the parasites from sago palm was 1:81.0 for 410 pupae observed. Preferences of both parasite species for food plants of the hosts were further demonstrated on the scale-

infested grapefruits and potato tubers. Progeny were obtained from scales on the grapefruit only.

According to Simmonds (1944), *C. bifasciata* preferred California red scale on orange to that on lemon. If scale size were the attractive factor in this case then the larger scales usually found on lemon would be preferable to the smaller scales usually found on orange. The factor that induces a higher mortality of the parasite on lemon than on orange or grapefruit may also repel the gravid female parasites. Differences in chemical content of different individuals of the same plant species may in part account for preferences.

Host selection by entomophagous insects has been studied extensively and in detail beyond the scope of this investigation by Flanders (1947a), Jackson (1937), Laing (1937, 1938), Lloyd (1938), Thompson and Parker (1927), Thorpe and Caudle (1938), Ullyett (1936), Varley (1941), and others.

Behaviour of adults.—The adult parasites, in particular *C. bifasciata,* exhibited abnormal activity when placed on leaves of sago palm. They invariably oviposited on one or two scales and then ran nervously over the leaves for several minutes. They spent considerable periods cleaning legs and antennae with the mouth parts while resting on the hairy, lower surface of the leaves. Ovipositions by *C. bifasciata* required an average of 5.3 minutes on sago palm compared to 3.0 on agave, 2.3 on yucca, 2.2 on lemon and 2.0 on orange.

California red scale on potato tubers was extensively used by the University of California (Flanders, 1947b, 1951) in the mass culture of *A. chrysomphali* and *A. lingnanensis,* though the present experiments showed preference by these species for hosts on grapefruits. Potato cuticle, beneath which the scale cover is forced during its secretion by the rotating pygidium, covers the veil of the scale through which these parasites must oviposit. Chemotactic stimulation was inevitably reduced by this protective film of cuticle. Reproduction of *C. bifasciata* and *H. rouxi* was scarcely effected, however, as these parasites detect their hosts at least partly by touch. The general outline of these covered scales was unaltered as the potato cuticle adhers to them closely.

Size.—As *C. bifasciata* and *H. rouxi* are solitary in their development, variations in size proportional to those of the host size were expected as shown in Table II. The measurements shown were averages of the progeny emerging from five weekly replicate infestations of scale on which each individual parasitization was observed. With conditions of light, temperature, host stage and host density practically identical and the food plant the only variant in the experiments, it is reasonable to assume that variations in the development of parasites and their behaviour when adult must be brought about indirectly by the influence of the plant upon the host insect. Thompson and Parker (1927), Ullyett (1936), and Flanders (1935, 1939c) made similar observations on other hosts and their parasites.

Sex ratio.—The sex ratios of progeny of *C. bifasciata* reared from replicate weekly infestations of California red scale living on six different host plants are given in Table III. The most interesting result was the consistent two to one (or better) majority of females over males from hosts on yucca and sago palm. Though some infestations of scale produced a preponderance of female parasites, in no cases were the results so consistent. The high ratios of females to males from yucca, sago palm, and agave, 5.26:1, 4.40:1, and 3.39:1 respectively, were in sharp contrast to those on *Citrus* spp. namely, 1.69:1, 1.29:1, and 0.81:1, on grapefruit, lemon and orange respectively. Brunson (1937), Clausen (1939), and Flanders (1937, 1939b, 1942b, 1944b, 1944c) made similar observations and

TABLE III
Sex ratios of *C. bifasciata* from red scale on different host plants

	Numbers of adults from five replicate infestations of scale										Totals		Percentage females
	1		2		3		4		5				
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
Yucca	2	5	2	10	2	7	2	12	0	8	8	42	84.0
Sago Palm	3	6	0	2	1	5	0	3	1	6	5	22	81.4
Agave	1	5	2	5	1	1	1	1	0	5	5	17	77.2
Grapefruit	1	5	4	6	6	8	1	0	1	3	13	22	62.8
Lemon	4	3	2	7	8	1	5	7	2	9	21	27	56.2
Orange	7	3	9	5	4	5	0	1	1	3	21	17	44.7

concluded that fertilization of the parasite eggs was influenced by some effect of the plant upon the host insect.

The occurrence of individual male adults of *H. rouxi* from grapefruit and from agave was not repeated in five replicate tests and was considered coincidental. Scales on potato tubers, from which the mother stock was reared, occasionally produced male parasites at a rate of one to about 70 females.

Life cycle.—The periods from egg deposition to emergence of adults of *C. bifasciata* and *H. rouxi* from five weekly infestations of scale on six different host plants are shown in Table I. These adults are the same individuals on which the data in Tables II and III are based. The life cycles of the two parasite species were approximately parallel on the various plants. Little correlation between the life cycles of the host and of the two parasites was apparent, however.

Mortality of immature stages.—Mortality of *C. bifasciata* was significantly higher during development in scale on sago palm than in scale on the other experimental host plants though lower than that reported by Flanders (1939a). The majority of dead, immature *C. bifasciata* on all plants, including sago palm, had died in the late pupal and early imaginal stages and a few had made emergence holes.

Records of complete mortality of *H. rouxi* where the host was reared on sago palm confirm reports by Flanders (1939a, 1942a), Smith (1942) and Smith and Flanders (1948). Of these dead parasites, 85 per cent had produced meconia but none had developed beyond this stage whereas most of those on the other plants had developed to at least the pupal stage. A few adults had partly emerged before dying.

The mortality of parasite eggs could not be detected in dead, dried scales and was thus not included in the data in Table IV.

High mortality of *C. bifasciata* and *H. rouxi* together with the shorter life cycle and greater reproductivity of their host insect when reared on lemon may be another factor in the greater damage by California red scale in lemon groves than in orange or grapefruit groves.

Flanders (1938, 1940) observed the indirect effects of the food plant of the host on other hymenopterous parasites.

TABLE IV
Percentage mortality of immature parasites in five replicate infestations of red scale on different host plants

	C. bifasciata	*H. rouxi*
Orange	7.3	4.8
Grapefruit	7.9	3.1
Yucca	9.1	10.7
Lemon	11.1	16.7
Agave	12.0	2.8
Sago palm	43.8	100.0

Reproductivity.—The progeny of *C. bifasciata* and *H. rouxi* from the five infestations of scale are shown in Table V as percentages of the observed ovipositions of the female parasites. A higher proportion of ovipositions produced progeny from scale on orange than from scale on the other test plants, though the difference was less than that observed by Simmonds (1944).

Longevity.—It may be seen from Table VI that the greatest average longevity of adults of *C. bifasciata* and *H. rouxi* was among those reared from scales on yucca. On this host plant, scales and parasites were larger than on other plants. The greater longevity of parasites from orange than of those from lemon confirmed reports by Simmonds (1944). Scales on agave produced parasites of the shortest survival period.

F2 generation from hosts on common food plant.—The sex ratios of second-generation *H. rouxi* from California red scale growing on potato tubers are shown in Table VII. These were the progeny of three female parasites from each of five replicate scale infestations on each of five host plant species. The data obtained were inconsistent and failed to show the existence of significant effects imposed by the food plant of the host on the second-generation parasites.

The surprising result was the large number of male progeny that normally occur only occasionally among adults of *H. rouxi*. Low night-time temperatures that resulted from failure of heating equipment for a few days were the only

TABLE V
Percentages of ovipositions on five replicate infestations of red scale resulting in emergence of healthy adults

Food plant of host	*C. bifasciata*	*H. rouxi*
Orange	48.7	45.9
Lemon	45.7	38.5
Yucca	45.4	33.8
Grapefruit	43.2	34.1
Sago palm	27.0	0
Agave	22.7	36.9

TABLE VI

Average longevity in days of adult parasites reared from four replicate infestations of red scale on different food plants

	C. bifasciata		*H. rouxi* ♀ ♀
	♂	♀	
Yucca	25	29	45
Orange	23	28	41
Lemon	19	27	44
Grapefruit	23	27	42
Sago palm	21	25	*
Agave	19	24	39

*No emergents.

known variations in conditions under which the mothers were reared. Only female adults emerged in each jar during the first 13 or 14 days and the males appeared during the following five or six days. Variations in temperatures rather than the effects of the food plants of the host appeared responsible for the sudden changes in the sex ratios. Flanders (1945a) concluded that the sexuality of *H. rouxi* was affected by the nutrition of the mother under certain temperature conditions. Other pertinent observations have been reported by Flanders (1942b, 1943c, 1945b) and Mittler (1946).

Prolificacy of the mothers as affected by the host plants of the hosts in which they developed is also shown in Table VII. The number of progeny of the large parasites from scales on yucca was 12.3 per cent greater than that on any other host plant.

TABLE VII

Progeny of *H. rouxi* females emerging from red scale on five plant species. Three females from each of five scale infestations were tested

	Progeny per three mothers from each of five parasitized infestations of red scale										Totals			Percentage females
	1		2		3		4		5					
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂+♀	
Grapefruit	10*	52	3*	18	2	41	0	36	0	44	15	191	206	92.6
Agave	2*	51	3	76	4	63	20	56	0	43	29	289	318	90.8
Yucca	2*	49	5*	56	28	108	2	82	0	25	37	320	357	89.7
Orange	10*	56	1	32	29	45	0	24	0	31	40	188	228	82.3
Lemon	5*	54	0	35	17	28	19	48	0	12	41	177	218	81.1

*Mothers subjected to constant 80°F. for the first one to four days of development followed by night-time extremes of 58°F. to 65°F. for twelve nights.

Summary

The food plant of California red scale, *Aonidiella aurantii*, affected the reproduction of its parasites both directly and indirectly.

Oviposition by the parasitic *Comperiella bifasciata* was retarded when the host scales were growing on sago palm. The effect of the potato tuber was direct in that during the formation of the scale cover it was overlaid with potato cuticle which formed a partial mechanical barrier to oviposition by *Aphytis chrysomphali* and *A. lingnanensis*.

The largest scales grown on *Yucca filipendula* produced adults of *C. bifasciata* and *Habrolepis rouxi* that were: larger, more predominantly of the female sex, of greater longevity, and more prolific than adults emerging from red scale growing on leaves of orange, lemon, grapefruit, agave, or sago palm. Mortality in the immature stages of these two species of parasites was highest in red scale grown on sago palm fronds where it was 100 per cent in the case of *H. rouxi*.

Experiments with *H. rouxi* to demonstrate an effect of the food plant of the host upon the sex ratio of an uniparental, bisexual parasite, suggested the need for further investigation. Present findings tend to confirm Flanders' conclusion that the food plant of the host insect may affect the sex ratio of the progeny when certain temperature conditions prevail.

Yucca filipendula proved to be the most satisfactory laboratory plant for rearing California red scale and its parasites.

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Alfalfa and Red Clover as Sources of Nectar and Pollen for Honey, Bumble, and Leaf-cutter Bees (Hymenoptera: Apoidea)[1]

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The most important factor affecting the densities of pollinating species of bees on alfalfa seed fields in southern Alberta is competing flowering growth (Hobbs and Lilly, 1954, 1955). This is a report on the relative attractiveness of red clover and alfalfa to honey, bumble, and leaf-cutter bees in southern Alberta. Observations were made on the first crops grown in each of two newly cultivated and irrigated areas near Hays; the fields were isolated from all other entomophilous crops by at least five miles of virgin prairie. A third series of observations was made on crops grown in the isolated river valley near Lethbridge previously described by Hobbs and Lilly (1955).

Methods

In 1953, observations were made on adjacent three-acre plots of LaSalle red clover and Ladak alfalfa that were in bloom in the isolated river valley. Sweet clover had been the principal source of food for the honey bees in the valley the two previous years (Hobbs and Lilly, 1955), and was still fairly abundant when observations were being made on the alfalfa and red clover plots. Observations were also made on the same varieties at Hays; here, a 25-acre field of red clover had been planted between a five-acre field of alfalfa and the virgin prairie; 32 hives of honey bees had been placed by a beekeeper about 300 yards from the crops for honey production and for pollination. In 1955, in another portion of this newly irrigated area, observations were made on a 27-acre field of LaSalle red clover and a seven-acre field of Vernal alfalfa two miles apart, but both bordering the same tract of virgin prairie. Twenty-five hives of honey bees had been placed beside the field of red clover for honey production and for pollination. Golden aster, *Chrysopsis villosa* (Pursh) Nutt., thistles, *Cirsium*

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spp., and gumweed, *Grindelia perennis* A. Nels., were the principal native sources of nectar and pollen on the prairie bordering the legume fields in the Hays area when alfalfa and red clover were in bloom.

Whenever bees were counted, the sex and the food preference (pollen or nectar) were recorded. Both years, numbers of native bees were counted at seven-pace intervals along the perimeter of each field to a depth of about five yards. In 1955 the honey bees were counted in the above manner; in 1953, they were counted on 50 one-square-yard areas chosen at random on both fields at Hays on two dates. Honey bees were not counted at Lethbridge. Because there was some doubt that the technical assistants distinguished *Bombus borealis* Kby. from *B. fervidus* (Fabr.) or *B. rufocinctus* Cress. from *B. huntii* Greene, numbers recorded for these species were grouped.

As the perimeter of the five-acre field of alfalfa was half that of the adjacent 25-acre field of red clover, the counts from red clover were halved. The length of the sampling area on the seven-acre field of alfalfa was two-thirds that of the 27-acre field of red clover, and the counts were adjusted accordingly.

Results and Discussion

Honey Bees

In 1953 the numbers of honey bees per square yard at Hays on July 10 and 13 were respectively 0.3 and 0.6 on red clover and 2.1 and 3.0 on alfalfa. Hence there were about five honey bees per unit area on alfalfa for every one on red clover. In 1955, the ratio at Hays was about 10 to one and there was no appreciable change in the ratio throughout the period when counts were made (Fig. 1).

Honey bees were not seen to gather pollen from alfalfa, and, because they almost invariably gathered nectar by inserting their tongues at the side between the keel and the standard petal, they accomplished very little pollination and even less cross-pollination (cf. Hobbs and Lilly, 1955). Although their densities on alfalfa were probably the highest ever seen by the writer in southern Alberta, no pod formation was evident until after August 4, when bumble bees began to visit the field in larger numbers (Fig. 2).

MacVicar, Braun, Gibson, and Jamieson (1952) showed that it was physically possible for honey bees to gather some nectar from red clover in eastern Ontario, but they and Braun, MacVicar, Gibson, Pankiw, and Guppy (1953) found no association between nectar volume or concentration and pollinating activities of honey bees on red clover. All of the honey bees observed on red clover during these and earlier observations on Ottawa or LaSalle red clover had pollen in their corbiculae. Relative numbers of honey bees on red clover and alfalfa (Fig. 1) indicated that alfalfa was the principal source of nectar, as few were seen on other bloom and all of those observed on alfalfa were gathering only nectar. Additional evidence that the honey bees did not utilize red clover as a source of nectar to any great extent was obtained from the beekeeper in 1955; although there was more than an acre of red clover bloom per hive, honey yields were so low that the operation was considered unprofitable. Presumably the honey bees did not make honey from red clover because their tongues were too short to extract more than the top one or two millimeters of the column of nectar and the small amounts gathered were hardly more than enough to satisfy the immediate nutritional requirements of the bees.

Bumble Bees

Bombus nevadensis Cress., *B. fervidus,* and *B. borealis* preferred red clover to alfalfa as a source of pollen, and apparently as a source of nectar (Figs. 2-4);

few members of those species were seen on any of the native bloom in the area. *B. huntii* was much less abundant at Hays than any of the above species and no flower preference for it is indicated in Fig. 3, but Fig. 4 shows that it preferred red clover to alfalfa as none were seen on alfalfa.

The continued fall in the densities of *B. nevadensis* on the red clover fields (Figs. 2 and 3) from the time counting was begun suggests that this species completes its brood-rearing cycle more quickly than does *B. borealis or B. fervidus;* on July 10, 1953 (Fig. 3), its foraging population was made up largely of workers whereas those of *B. borealis* and *B. fervidus* were still mostly queens. There were more of *B. borealis* than of all other species combined on July 24 (Fig. 3), when most of the foragers were workers, and there were more of *B. fervidus* than of all other species combined on July 31 (Fig. 3), when new males and queens of all three species were becoming numerous, suggesting that *B. borealis* completes its brood-rearing cycle before *B. fervidus.*

In 1955, numbers on alfalfa almost equalled those on red clover toward the end of the season (Fig. 2), probably because little bloom remained on red clover as compared to alfalfa. In 1953, excess irrigation helped to maintain bloom on both fields at Hays, and it is unlikely that lack of bloom on red clover forced the bees to alfalfa for food; however, late in the season, when the numbers on alfalfa were at their highest, the foraging population was mostly new males and new queens. For example, at Hays, on August 15, 1955, when the writer made the counts alone, seven queens, four males, and four workers of *nevadensis* and 11 queens, 20 males, and nine workers of *fervidus* were recorded. New males and new queens gather only nectar and apparently do not have the decided preference for red clover shown by workers or overwintered queens, which gather both pollen and nectar. When bumble bees gather only nectar from alfalfa, they accomplish less tripping than do pollen-collecting workers or overwintered queens. It is likely that the size of the nectar-gatherer and the amount of tripping it accomplishes are positively correlated; large clumsy ones trip more alfalfa flowers than do small ones. Therefore, to accomplish the same amount of pollination, densities of bumble bees must be higher when the foraging group is made up largely of new, nectar-collecting males and queens.

Leaf-cutter Bees

No female leaf-cutter bees, *Megachile* spp., were seen to visit red clover for nectar or pollen. They have never been recorded on *Trifolium* spp. in southern Alberta and only a few have been recorded on sweet clover, *Melilotus* spp. (Hobbs and Lilly, 1954). The total numbers of males and females of leaf-cutter bees, mostly *M. dentitarsus* Sladen at Hays and *M. frigida frigida* Sm. at Lethbridge, on the margins of alfalfa fields in 1953 were:—

	Hays				Lethbridge	
	July			August	July	
	10	24	31	14	16	29
Males	0	1	22	0	2	0
Females	0	3	6	5	0	5

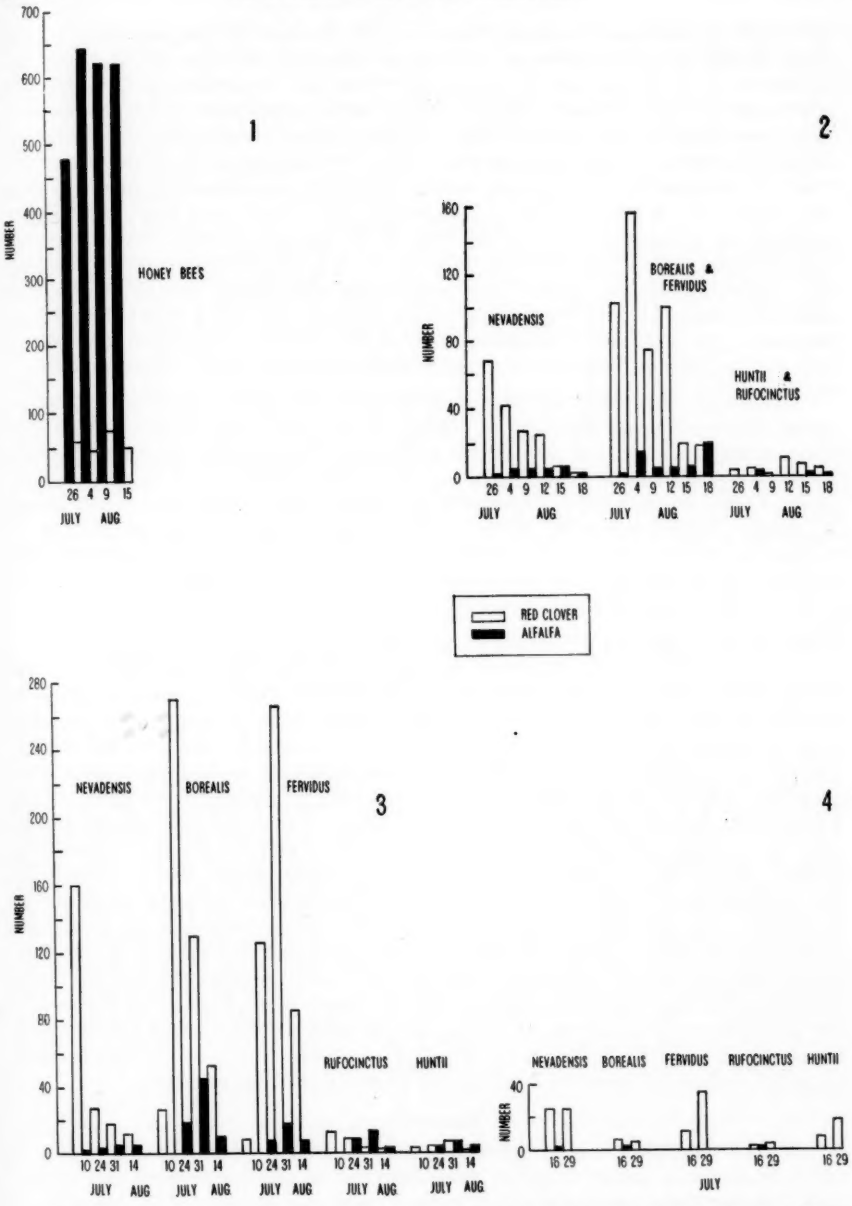

Fig. 1. Relative densities of honey bees on the alfalfa field and the red clover field at Hays, Alberta, 1955.

Fig. 2. Relative densities of bumble bees on the red clover field and the alfalfa field at Hays, Alberta, 1955.

Fig. 3. Relative densities of five species of bumble bees on the red clover field and the alfalfa field at Hays, Alberta, 1953.

Fig. 4. Relative densities of five species of bumble bees on the red clover plot and the alfalfa plot in the river valley near Lethbridge, Alberta, 1953.

The high proportion of males at Hays on July 31 reflected the beginning of the flight period of *M. dentitarsus*. The extremely low densities at Hays can be attributed to an abundance of competing bloom on the prairie, and to the fact that virgin prairie normally supports only a small population of leaf-cutter bees until food (alfalfa) and nest-building materials (trees and shrubs) are grown on irrigated portions bordering the prairie. The low densities at Lethbridge resulted from an abundance of competing bloom, from the extermination program that was carried out in 1951 and 1952 (Hobbs and Lilly, 1955), and from a flood that covered the alfalfa field and its environs in the spring of 1953. No leaf-cutter bees were recorded from alfalfa at Hays in 1955, probably because those making the counts moved too quickly and approached too closely to the foliage and disturbed them, because competing native growth on the prairie bloomed so profusely that few females were attracted to the alfalfa, and because populations had not had time to build up as a result of the introduction of abundant food.

Although *M. dentitarsus* and *M. frigida* are not attracted to red clover or sweet clover, they are attracted to certain of the native species that bloom near their nesting habitats. *M. dentitarsus* will gather from gumweed rather than fly to the irrigated alfalfa fields bordering its nesting habitat, and *M. frigida* will gather nectar and pollen from fireweed, *Epilobium angustifolium* L., in preference to alfalfa (Hobbs and Lilly, 1954). Hence, ideal conditions for pollination of alfalfa by leaf-cutter bees in southern Alberta are droughty conditions that suppress the production of bloom on their native food plants and force them to fly to the irrigated alfalfa fields.

Relation of Pollination to Seed Production

In 1953, 226 pounds of plump seed per acre were harvested from the red clover field at Hays, despite poor agronomic practices that probably resulted in the loss of over half of the seed. Less than 100 pounds of plump seed per acre were harvested from the alfalfa field, although it was only one-fifth the size of the red clover field and should therefore have produced an amount closer to its potential yield if the pollinators had been present in sufficient numbers. As a killing frost did not occur until October 4, most of the seed on both crops had time to mature, and most of the pollination of alfalfa by the few late-flying bumble bees (Fig. 3) and the leaf-cutter bees (leader table above) resulted in the production of mature seed. In 1955, the temperature dropped to 20°F. on September 10, and the maturing seeds in the pods that resulted from the pollination of alfalfa flowers by the few late-flying bumble bees (Fig. 2) were killed; only 40 pounds of plump seed per acre were harvested from this field. Bumble and honey bee pollination on the red clover field (Figs. 1, 2) resulted in the production of an average of 410 pounds of seed per acre on an acreage four times the size of the alfalfa field, showing that pollination on the clover field occurred sufficiently early to result in the production of mature seed.

Summary

In southern Alberta, although honey bees preferred red clover to alfalfa and native flowers as a source of pollen, their densities on red clover were low apparently because they could not utilize it as a source of nectar. The densities of nectar-collecting honey bees were high on alfalfa, but their visits to alfalfa flowers did not result in enough cross-pollination to produce a crop of seed of commercial importance.

Bumble bees preferred red clover to alfalfa and native flowers as a source of both pollen and nectar during the part of the blooming period when pollination resulted in the production of mature seed. *Bombus borealis* was considered the

most important bumble bee pollinator of red clover because its brood rearing cycle coincided with the blooming of red clover better than did those of *B. nevadensis* or *B. fervidus*.

Leaf-cutter bees did not utilize red clover for food. They did not show the decided preference for alfalfa that bumble bees showed for red clover, and their services as pollinators were largely lost because their native food plants bloomed profusely in their nesting habitat.

Acknowledgments

The writer wishes to express his appreciation to officers of the Lethbridge laboratory as follows: to Mr. C. E. Lilly, who was formerly associated with this project and who assisted in the sampling in 1953, and to Drs. N. D. Holmes, R. W. Salt, and G. E. Swailes, who criticized the manuscript.

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Studies of the Byron Bog in Southwestern Ontario
I. Description of the Bog[1]

By W. W. JUDD[2]

Introduction

The Byron Bog is a sphagnum bog situated about three miles west of London and one mile northeast of Byron, Ontario in a depression adjacent to the southwest corner of Oxford Street and Hyde Park Sideroad in London Township of Middlesex County (Fig. 1). During the past it has been variously designated as "The Spruce Swamp", "Foster's Bog" and "Redmond's (sometimes erroneously spelled "Redman's") Swamp" or "Redmonds' Bog". Woolverton (1900) described it briefly in an account of a trip to the bog by members of the Geological Section of the Entomological Society of Ontario in 1899: "A number of the members of the section visited a peat bed, situated 3 miles west of London at Redmond's farm. It lies in a low spot bordered by high hills on the east and north. Towards the south a barrier not more than a few feet in height isolates it from the River Thames. In the centre is a pond of clear spring water over 60 feet in depth . . ." The bog has attracted the attention of local naturalists, particularly members of the McIlwraith Ornithological Club of London, who have studied various features of its fauna and flora, e.g. Dearness (1907), Judd (1956a), Saunders (1932) and Saunders and Dale (1933).

In the spring of 1956 an investigation, of which the present paper is the first report, was begun on the biology of the bog, particularly with reference to the insects occurring in it. This bog lies at or near the northern border of the Carolinian Zone in Ontario (Fox and Soper, 1954; Judd, 1955) and thus affords an opportunity to investigate the insects occurring in an ecological unit charac-

[1]Contribution from the Department of Zoology, University of Western Ontario: a project supported by funds from the government of Ontario granted through the Ontario Research Foundation.

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teristic of the more northern coniferous forest, but here situated at the edge of the Beech-maple Forest Region (Braun, 1950). Braun points out that bogs in this region are relics and are in sharp contrast to the surrounding deciduous forest. During the course of the work in 1956 a collection was made of the predominant plants in the bog. They were identified by Dr. J. H. Soper, Curator of the Herbarium, Department of Botany, University of Toronto, who retained specimens for that institution. Duplicate specimens are retained in the herbarium of the writer and in the following account the accession numbers of these specimens are noted following the names of the plants.

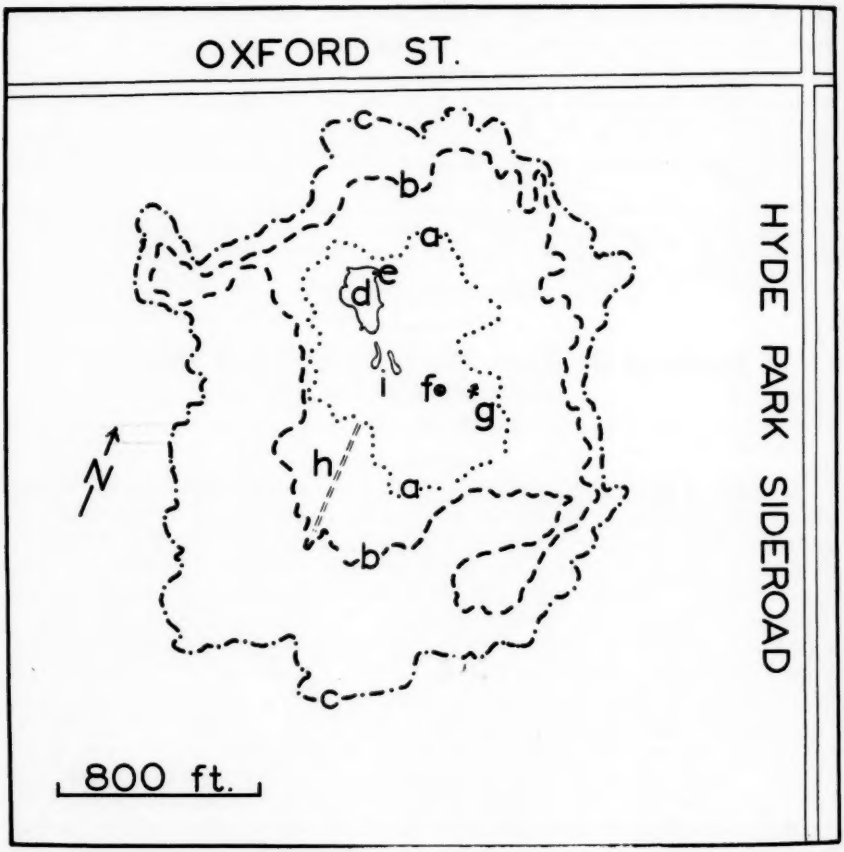

FIG. 1. MAP OF BYRON BOG

a-a: outer border of open floating bog
b-b: outer border of lower, damp woods
c-c: outer border of open wooded slopes
d: Redmond's Pond
e: location of tent-trap
f: location of baited insect trap
g: location of co-ordinate point—42°58′15″N, 81°19′15″W
h: drainage ditch
i: small ponds in bog

Description of the Bog

The hollow in which the bog is situated is surrounded by wooded slopes the outer limits of which are indicated by c-c in Fig. 1. A variety of deciduous trees and shrubs such as White Elm, Bur Oak, Red Oak, a few Chestnut Oak, Hackberry, Silver Maple, Black Cherry, Willow, Hawthorn, Chokecherry, Nannyberry, etc. comprise this wood.

The wooded slopes give way to a lower wooded region, permanently damp or flooded, whose outer limit is designated by b-b and inner limit by a-a (Fig. 1). In this region there is a cover of trees and shrubs, thicker toward its outer limits and thinner toward its inner limits. The predominant feature of the vegetation here is the dense growth of the Alder-buckthorn, *Rhamnus Frangula* L. (567) with a scattered overgrowth of taller trees including Silver Maple, White Pine, and White Birch. The inner limit of this region is occupied mainly by Larch, *Larix laricina* (DuRoi) K. Koch and Black Spruce, *Picea mariana* (Mill.) BSP. over an undergrowth of Leather-leaf, *Chamaedaphne calyculata* (L.) Moench (557) growing in *Sphagnum*. A few shrubs of Purple Chokeberry, *Pyrus floribunda* Lindl. (562) and clumps of the Black Highbush-blueberry, *Vaccinium atrococcum* (Gray) Heller (558), and Black Huckleberry, *Gaylussacia baccata* (Wang.) K. Koch (565), grow among the conifers. This region is traversed, toward the south, by a drainage ditch (Fig. 1-h).

The central, open floating bog, the outer limits of which are indicated by a-a, is based on a thick layer of *Sphagnum*. Woolverton (1900) measured the thickness of the peat layer beneath the sphagnum in winter and found that toward the centre of the bog it was at least 60 feet deep and that in the outer zone there was 8 to 20 feet of peat. A few short Larches and Black Spruce are scattered over the bog. Almost the whole area of this floating bog is densely covered by *Chamaedaphne calyculata*, which extends right to the edge of the central pool (Fig. 1-d) where the branches of the bushes reach over the water. The bushes of *C. calyculata* grow from rounded cushions, as much as two feet high, composed of *Sphagnum* and crowned with other mosses. This association of *C. calyculata*, called by Dansereau and Segadas-Vianna (1952) the "*Chamaedaphnetum calyculatae* association", is described by the same authors as being characteristic of the "consolidation" or "settlement" stage of a bog. The consolidation in the Byron Bog has evidently been furthered by the partial draining of the bog following the construction of the ditch (Fig. 1-h). Between the cushions supporting the Leather-leaf grow Pitcher-plants, *Sarracenia purpurea* L. (569) and tall stalks of the Tawny Cotton-grass, *Eriophorum virginicum* L. (586); and on the sides of the cushions are the Round-leaved Sundew, *Drosera rotundifolia* L. (582) and the Small Cranberry, *Vaccinium Oxycoccos* L. (573).

At intervals through the *Chamaedaphnetum calyculatae* association there are open areas largely devoid of *C. calyculata* and with the sphagnum levelled off rather than cushioned and including shallow pools of open water. Samples of water taken from a pool in the fall of 1956 showed a pH of 4.2. Toward the centre of these open areas are closely-set mats of the Sundew, *Drosera intermedia* Hayne (580), clumps of Bladderwort, *Utricularia cornuta* Michx. (576), and scattered plants of Grass-pink, *Calopogon pulchellus* (Salisb.) R.Br. (578), Beard-flower, *Pogonia ophioglossoides* (L.) Ker (574), Beak-rush, *Rhynchosopora alba* (L.) Vahl (584) and Bog-rush, *Juncus canadensis* J. Gay (585). Around the edges of the open areas are bushes of Bog-laurel, *Kalmia polifolia* Wang. (561) and Bog-rosemary, *Andromeda glaucophylla* Link (560) and scattered plants of the Large Cranberry, *Vaccinium macrocarpon* Ait. (579) and Marsh-St. John's-wort, *Hypericum virginicum* L. (583).

Toward the northwest corner of the floating bog is the open pond (Fig. 1-d) called Redmond's Pond by Dearness (1907). It is completely surrounded by the growth of Leather-leaf growing in *Sphagnum*. Its surface is devoid of vegetation except in small bays around its circumference where there are growths of Spatterdock, *Nuphar advena* (Ait.) Ait. f. (571), and Bladderwort, *Utricularia vulgaris* L. (581) and a sparse accumulation of the floating fronds of the Duckweed, *Lemna minor* L. and Water Flax-seed, *Spirodela polyrhiza* (L.) Schleid. The pH of the water, measured in the fall of 1956, was 5.3. Southward from Redmond's Pond, toward the drainage ditch, there is a series of smaller ponds and pools (Fig. 1-i) surrounded by Leather-leaf and *Sphagnum* and supporting an abundant growth of *Nuphar advena* and *Utricularia vulgaris*. Among these smaller ponds are stands of the Common Cat-tail, *Typha latifolia* L. together with a few clones of the Blue Flag, *Iris versicolor* L. (577) and scattered plants of the Swamp-pink, *Arethusa bulbosa* L. (570), loosely embedded in the sodden *Sphagnum*.

Methods of Study

The map (Fig. 1) was enlarged from a tracing of an aerial photograph taken in May, 1956 for the use of the Planning Board of the Township of London. The position of the co-ordinate point shown on the map was calculated by comparison with the "St. Thomas Sheet" (west half) of the National Topographic Series. Measurements of pH were made with a Beckman pH meter. Insects were collected in a variety of ways. Adult insects emerging from the water were trapped in a tent-trap of the sort used by Miller (1941). This trap covered four square feet of surface and was anchored in a small bay at the northeast corner of Redmond's Pond (Fig. 1-e). A baited trap, described by Judd (1956b), was set out in an open area in the *Chamaedaphnetum calyculatae* association (Fig. 1-f) to trap blowflies, biting flies etc. Each day a circular sweep of an insect net, held at arm's length, was made through the tops of the bushes in the *Chamaedaphnetum calyculatae* association in order to study the seasonal changes in the insect population of that association. As opportunity afforded insects were caught in flight with the net, picked from trees, shrubs and plants and trapped in poison jars clapped over foliage.

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Book Review

THOSE OF THE FOREST. By Wallace Byron Grange, 314 pages, illustrated by Olaus J. Murie, 1953. The Flambeau Publishing Company, Babcock, Wisconsin. Price $4.75.

Wallace Grange, who was Wisconsin's first Superintendent of Game, is well known for his work on grouse, rabbits, and animal cycles. He is the author of two previous books, *Wisconsin Grouse Problems* (Wis. Cons. Dept., 1948), and *The Way to Game Abundance* (Scribner's, 1949), and of numerous technical and popular articles.

In the present book written in simple, often poetic, language he conducts the reader through the changing seasons in a typical part of the forest,—ridge, softwood swamp, and beaver pond. The location is probably Wisconsin but biologists in central or eastern Canada will feel quite at home there, both with the plant associations and with the various species of insects, birds and mammals that are encountered. The central figure is a snowshoe rabbit and many of the events that unfold in the "living rhythm of the forest" are seen through his eyes.

At first glance, it may seem that this is scarcely an appropriate book to be reviewed for an entomological journal. It is essentially, however, a book on ecology and on animal numbers. Defoliating caterpillars, biting flies, ants and spiders receive frequent attention as a part of the ecosystem. And what entomologist has not been impressed by the interrelations among organisms and by the need to study insect ecology on a very broad basis? Again, the problems of population dynamics have many features in common whether we are primarily concerned with an insect, a bird, or a mammal. Wildlife workers like Aldo Leopold and Wallace Grange have been much more successful than have entomologists in expressing these fascinating problems in a colourful, natural language which should appeal alike to entomologists, foresters, hunters, or even casual visitors to the forest.

Most chapters open with a description of one of the seasons and its phenology and the author has captured so well the sights, sounds, and smells of the different seasons that the reader who is familiar with the forest will have the feeling he is there. Next some seemingly simple event occurs—a rabbit is captured by an owl, or a grove of poplars is defoliated by caterpillars. These events are often cruel and death through predation, hunger, or adverse physical elements is frequent and certain. Central figures in the drama are plagued in summer by mosquitoes, ticks and various internal parasites. These features of the book will not appeal to those who enjoy conventional nature stories where the pursued always escapes the pursuer and all wild animals are strong and healthy. Considering the rapid turn-over in natural populations, however, especially in species near the bottom of the Eltonian pyramid, a realistic picture of nature could hardly be otherwise. The author then speculates on the ramifications of this event and its effects on other animals and plants. In these passages we see the balance of nature and the oneness of all elements of the ecosystem. We also see that all events in nature, from photosynthesis to the ultimate predation, are simply transfers of energy from one form to another and that the ecologist may eventually be able to express them as such. Finally, the chapter may close with several pages that can only be described as philosophical—the "Why?" and the "Whence?". These are designed to stimulate rather than inform and the interrogation mark is used more frequently than the period. Perhaps one of the best examples is the discussion of chance and natural laws in Chapter 10, where we find ideas like those of George Wald on the certainty of occurrence of an extremely improbable event, when probability is multiplied by time.

It is to the student of animal numbers that the book will have its greatest appeal. Such technical terms as "natural control" or "population dynamics" are not used; nor are any references cited. It is apparent in every chapter, however, that the author is fascinated by the mysteries of animal population. The climax comes in Chapter 12, where the snowshoe population reaches its peak and experiences the inevitable collapse. It has been suggested in earlier chapters that some species (deer) are controlled by the winter food supply, others (spruce grouse) by enemies and others by weather, but here it seems that the author is one of those who believe in the multiplicity of factors contributing to population decline. The rabbit population is overtaken by predator populations. The hordes of rabbits exhaust the available food supply. The caprices of winter weather put higher browse beyond their reach. The processes of forest succession and growth have made the habitat less suitable for rabbits than in former years. (The effects of this factor have been neglected by many population students, who have tended to regard the forest itself as a very stable environment). Finally, the rabbits have been controlled, basically, by the limitations of their species. Some years ago W. R. Thompson wrote that "Natural control is primarily due to the intrinsic limitations of the organisms themselves", but the real meaning of this only becomes clear when we see the situation portrayed as vividly as it is on pages 244-247.

The final chapters of the book take us through geological time and forest succession with the "ancient rabbit" to learn how this particular piece of forest came to exist in its present form and how the rabbit came to be there.

"Those of the Forest" is a book that will provide much enjoyment and stimulation for the entomologist, and particularly for the forest entomologist.

R. F. Morris

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